Understanding drivers of long-term change in semi-natural habitats

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ABSTRACT

Biodiversity has declined considerably across the globe and this is largely due to the destruction and degradation of habitats, which is predicted to continue in the future. Understanding the dynamics and mechanisms behind habitat loss and degradation can help predict future change and plan potential ameliorative actions, such as restoration. Long-term change studies have proved exceptionally valuable for understanding these drivers, though few studies examine more than two snapshots in time. As a result the current knowledge of these drivers of change, their trends and the resulting responses is deficient. This thesis examines the long-term drivers of habitat loss and quality in southern England over multiple time periods for a range of semi-natural habitats. The research questions are as follows;

(i) What are the spatio-temporal patterns and drivers of habitat loss?
(ii) Does habitat loss lead to extinction debts across a range of habitat types?
(iii) What are the temporal patterns and drivers of vegetation change in calcareous grasslands?

Chapters 2 and 3 address the first research question by exploring the dynamics of habitat change over time for a rural county in southern England. Historical surveys and contemporary spatial datasets were used to construct a habitat time-series dataset for over 3700 sites across the county between 1930 and 2015. This dataset was then used to model landscape maps for the whole county in 1950 and 1980 using the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) Scenario Generator tool. These chapters revealed both the spatial and temporal patterns of loss, which were largely non-linear for the majority of semi-natural habitats between 1930 and 2015. The greatest losses occurred between 1930 and 1980, which coincided with the period of most rapid agricultural intensification in the UK. However, even after this period semi-natural habitats were still being lost, despite so few sites remaining. Statutory protection was important for retaining semi-natural habitats, which provides evidence for their effectiveness and the need for continued protection in the future.

The fourth chapter utilises the datasets produced in the previous two chapters to test for plant community extinction debts (delayed species extinctions following habitat degradation) in three of the semi-natural habitats (calcareous grassland,

heathland and broadleaved woodland), thus addressing the second research question. A key knowledge gap is addressed by comparing three different extinction debt methods. These three species-area relationship methods differ in their data requirements, with the first two using information on past and current habitat area alongside current species richness, whilst the last method also requires data on past species richness. The most data-intensive method identified extinction debts across all three habitats for specialist species, whilst the other methods did not. This suggests that extinction debts may be under-reported, which has important implications for employing conservation action.

Chapters 5 and 6 address the third research question by focusing on long-term change and drivers of habitat quality using calcareous grassland as a case study. Both chapters used vegetation survey data from National Nature Reserves (NNR) spanning between the 1970s and 2010s. Chapter 5 used vegetation and soil data collected at Parsonage Down at three time points (1970, 1990 and 2016) and found declines in species richness, diversity and shifts in species composition across the survey period. Nitrogen deposition may have contributed towards community changes between 1970 and 1990, as indicated by the change in soil properties and the associated decline in species diversity. However, between 1990 and 2016 vegetation change is likely to be largely attributable to a reduction in grazing pressure, indicated by the increase in taller species and a decrease in grazing tolerance. Chapter 6 examined vegetation change alongside detailed grazing records across multiple time periods at Martin Down. Although a significant shift in the grazing regime was detected, whereby grazing previously occurred across all seasons to now predominantly occurring in autumn and winter, the vegetation communities remained largely consistent. This suggests that these vegetation communities are robust to changes in seasonal grazing providing that sufficient grazing pressure is provided within the year.

The findings presented in this thesis demonstrate the importance of long-term data and the value of analysing multiple intermediate time periods to identify trends in drivers of change and their responses.

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AUTHOR'S DECLARATION

I confirm that this thesis is my own work, with the exceptions of the manuscripts below. As senior author on all the papers below, I led all aspects, including idea development, data collection, analysis and interpretation. I also led the preparation of these manuscripts. Where other sources of data were used in this thesis this is acknowledged and referenced accordingly.

Chapter 2 is published in collaboration with my supervisors and co-authors as:

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LER performed data handling, spatial and statistical analyses and wrote the manuscript. SCLW helped digitise data. ACN and JMB advised on appropriate analyses and interpretation of results. CSR supplied the land cover data. All authors discussed the results and commented on the manuscript.

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CHAPTER 1

INTRODUCTION

This thesis uses a range of datasets including field surveys and spatial data, to examine the long-term drivers of habitat loss and quality, over multiple time periods for a range of semi-natural habitats in the UK. This introductory chapter, outlines the global biodiversity crisis and explains why long-term data is critical for understanding the mechanisms of biodiversity loss. It subsequently introduces the semi-natural habitats examined in this thesis and explains why the study system is an ideal area to explore loss and degradation in such habitats. The chapter then concludes with the thesis aims and an outline of the subsequent chapters.

1.1. THE GLOBAL BIODIVERSITY CRISIS

Biodiversity underpins ecosystem function and the provision of ecosystem services, such as provisioning (food, water), regulating (air quality, pollination) and cultural services (recreation, spiritual) (CICES 2017). Human societies have often underestimated the importance of ecosystems and the benefits they provide (Chan et al. 2006) and over the past 500 years we have seen considerable declines in biodiversity. It is estimated that we are losing around 11,000 to 58,000 species annually (Dirzo et al. 2014) and the rate of this loss does not appear to be slowing (Pereira et al. 2010, Newbold et al. 2015). These global declines in biodiversity are largely attributed to anthropogenic factors including overexploitation, habitat destruction and degradation, pollution, invasive species and climate change (Butchart et al. 2010, Dirzo et al. 2014). Habitat destruction through land-cover change has been identified as one of the most important drivers of biodiversity loss across the globe and this is not only predicted to continue (Powers and Jetz 2019), but it is also forecast to have the largest effect in the future (Sala et al. 2000). Understanding habitat destruction as a mechanism of biodiversity loss, is therefore as important as ever. Furthermore, habitat destruction interacts with other drivers of biodiversity decline, some of which are becoming increasingly important, such as climate change (Arneth et al. 2020).

Habitat destruction and degradation in terrestrial ecosystems encompass a wide range of changes to natural and semi-natural habitats by human activities. It is estimated that 75% of the total global land surface is described as severely altered (IPBES 2019). Unlike other drivers of biodiversity loss, such as pollution, which is considered to have a larger impact in northern temperate areas near cities, habitat destruction and degradation have occurred across multiple biomes (Sala et al. 2000). The conversion of natural and semi-natural habitats to agriculture has been the most important habitat change globally. In temperate regions, semi-natural grasslands have been converted to arable land, whilst in the tropics large expanses of forests have been removed for cattle ranching and plantations for oil palm (Fearnside 2005, Hansen et al. 2009). Urbanisation is becoming increasingly important as a driver of biodiversity loss and although currently urban areas only cover 3% of the land globally (Liu et al. 2014), their extent is expected to triple by 2030 (Seto et al. 2012). Habitat degradation is often associated with destruction, however unlike destruction, degradation is considered a gradual decline in habitat quality over time, which can be more subtle and difficult to detect. One of the most important drivers of degradation in habitats across Europe and North America is eutrophication (nutrient enrichment through fertilization or nitrogen deposition), which has led to declines in plant richness and diversity and community shifts in a number of habitats (Maskell et al. 2010, van Dobben and de Vries 2017, Peppler-Lisbach et al. 2020). Inappropriate management of natural and semi-natural habitats can also result in degradation. For example, in parts of South America, Africa and Asia, high grazing pressure has resulted in the degradation of grassland ecosystems (Marino et al. 2020, Yousefi et al. 2020).

The destruction and degradation of ecosystems relate strongly to disturbance theory, which was first defined by White and Picket (1985) as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment”. Disturbances are often defined as either “pulse” disturbances, which are abrupt changes or “press” disturbances, which are continuous gradual changes (Newton 2021). Habitat destruction through land-use change, for example the conversion of a semi-natural grassland to agricultural land is considered a pulse disturbance. On the other hand, habitat degradation, for example the decline in vegetation quality over time due to eutrophication is defined as a press disturbance.

Land-cover change, such as the conversion to agriculture or urban, leads to the direct loss of habitats, but also results in the fragmentation of remaining semi-natural habitats, whereby habitats are reduced to smaller patches that are more isolated within a matrix of human altered land-cover (Fahrig, 2003). The impact of habitat loss, degradation and fragmentation can lead to the immediate extinction of species; however many populations respond slowly to environmental change. This means populations living close to their extinction threshold might survive for long time periods before they go extinct, even without any further habitat changes. This phenomenon is described as an “extinction debt” (Tilman et al. 1994). Although the number of studies examining extinction debt have increased in recent years, the conclusions are often varied (Kuussaari et al. 2009, Figueiredo et al. 2019). Extinction debt is challenging to investigate empirically and the differences in the methodologies employed may explain the inconsistent results reported across such studies. There is a need to understand whether there is an issue with the methods used or whether there really is no extinction debt, in order for the impacts of habitat destruction and degradation to be fully understood, particularly as this driver is predicted to continue to have the largest effect in the future.

Although habitat destruction and degradation as a general mechanism for biodiversity loss are well known, knowledge on the rates and spatio-temporal patterns of these drivers is still limited. This information is essential for halting the decline in biodiversity through the development of appropriate management strategies and implementation of conservation action such as restoration. Long-term data provides an opportunity to assess drivers of biodiversity loss through time, by providing a baseline against which the current trends in biodiversity can be compared.

1.2. THE NEED FOR LONG-TERM DATA

The definition of long-term is variable across the ecological literature with some using the phrase to describe a five-year experiment (Gholz et al. 2000, Niklaus et al. 2001), while others use long-term in the context of change over multiples decades

(Silvertown et al. 2006, Markle et al. 2018) or even centuries (Herben et al. 2006, Boivin et al. 2016). In the context of assessing drivers of biodiversity decline, the further back in time considered, the greater likelihood of understanding the impacts of habitat destruction on global biodiversity. However, the time period assessed is usually governed by the availability of data, which has important implications for the reporting of biodiversity change over time. Many recent long-term studies tend to focus on biodiversity change over the last forty to fifty years at best. For example, in Germany, Hallmann et al. (2017) revealed a 76% decline in flying insect biomass in protected areas between 1989 and 2016. Similar time periods have also been used to assess insect trends in Great Britain (1980 and 2013) (Powney et al. 2019), Puerto Rica (1976 and 2012) (Lister and Garcia 2018) and the US (1975 and 2019) (Crossley et al. 2020). Although there are a few exceptions to this (e.g. Hambler et al. 2011 focussed on change in the 19th and 20th century), the majority of studies examine biodiversity change after considerable habitat destruction has already occurred, thus ignoring potential species losses during earlier land-cover changes. This highlights the importance of using long-term datasets that go back far enough in time to incorporate periods of significant land-cover change.

The majority of long-term research on habitat loss and degradation has focused on singular major changes often determined when assessing two snapshots in time (Taverna et al. 2005, Mahmoud et al. 2019). While it is important to recognise these major land-cover changes, identifying the temporal patterns of such changes is key to improving our understanding of the impact on biodiversity. This is because land-cover change is not a simple process and instead a particular area may undergo multiple land-cover changes over time. For example, a semi-natural grassland may be converted for crop production, only to be restored to a different grassland community decades later (Walker et al. 2004). By considering long-term change over multiple time periods, information on the frequency and sequence of land-cover changes, the time span each land-cover type extends, and the magnitude of difference between land-cover types can be understood (Watson et al. 2014). These factors are important aspects of disturbance theory. The type of disturbance, as well as the extent, intensity and magnitude of the disturbance can vary across space and time (Grimm et al. 2017). Moreover, the current response to a disturbance event can be dependent on the spatial and temporal distribution of disturbances in the past (Raffa et al. 2008), thus emphasising the need for long-term data.

Many studies which consider land-cover change or habitat loss across more than two snapshots in time often focus on a single habitat type (Rose et al. 2000, Cousins 2009, Margono et al. 2014, Mesfin et al. 2020). However, in order to understand the differences between land-cover changes, multiple habitats within a landscape need to be assessed. This is consistent with the framework established by Peters et al. (2011), which supports the quantitative comparison of different disturbance impacts across different types of ecosystems. An example of evaluating multiple habitats can be seen in the UK with the Countryside Survey, which is a comprehensive dataset that regularly assesses the extent and condition of broad habitats using 1km survey squares (Barr et al. 1993, Carey et al. 2008). Although multiple time periods are examined within this dataset, the first survey was undertaken in 1978, which returns to an earlier issue, whereby considerable land intensification has already occurred in the UK by this point. There is therefore a need to consider habitat loss both over longer time periods, but also at multiple intervals, so that the spatio-temporal dynamics of habitat destruction can be identified.

1.3. THE IMPORTANCE OF SEMI-NATURAL HABITATS

Semi-natural habitats have high conservation importance across many parts of the world. Semi-natural habitats are defined as those which were created by traditional human activities and require maintenance through management, such as grazing, coppicing, cutting or burning (Poschlod and Wallis de Vries 2002). In the UK there are several systems used to classify habitats and these have largely been devised to enable protection of habitats or for survey reasons, for example Phase 1 Habitat Classification and the National Vegetation Classification (Rodwell 1992). The Priority Habitats Classification was developed as part of the UK Biodiversity Action Plan and categorises semi-natural habitat types which are considered as being the most threatened due to rarity or rate of decline. The Priority Habitats are nested within the Broad Habitat framework (Jackson 2000), which defines terrestrial and freshwater types based upon descriptions that were agreed by the UK Biodiversity Group in 1995. In this thesis the Broad Habitats Classification is used to define the semi-natural habitats of interest; namely acid grassland, broadleaved, mixed and yew woodland (hereafter broadleaved woodland), calcareous grassland, fen, marsh and swamp, dwarf shrub heath (hereafter heathland) and neutral grassland. The Broad Habitat framework was chosen as the classification system for this thesis because it corresponded well with other spatial datasets, such as the Centre for Ecology and Hydrology (CEH) Land Cover Map 2015 (Rowland et al. 2017). Descriptions of the Broad Habitats types included in this thesis and how these relate to Priority Habitats can be found in Table 1.1.

These semi-natural habitats were selected for this thesis because they are of considerable conservation importance in the UK, usually because they are species-rich or the species contained within them are habitat specialists and/or rare. For example, heathland is not a particularly species-rich habitat, but it supports a number of specialist species, many of which are rare or are only found in heathland (English Nature 2002). On the other hand, calcareous grasslands are considered species-rich habitats, particularly in relation to their vascular plant community, which is very diverse (Wilson et al. 2012). However, if all life-forms are considered, broadleaved woodlands are one of the richest habitats, supporting a huge range of species, again with many of these considered rare or threatened (Lake et al. 2014). These semi-natural habitats are also important for the wide range of ecosystem services that they deliver, including pollination, timber production, carbon storage and cultural value (Quine et al. 2011, Cordingley et al. 2015, Holland et al. 2017, Bengtsson et al. 2019).

Despite the importance of these semi-natural habitats, there have been significant declines in their extent during the twentieth century in the UK. In England and Wales, for example, an estimated 97% of semi-natural grassland was lost between 1932 and 1984 (Fuller 1987), whereas an estimated 80% of lowland heathland has been lost since 1800 in the UK (Webb 1986). Although estimates exist for the loss of particular semi-natural habitats over time, information on the trends and drivers of such losses, or the differences between them is not fully understood. This is also true regarding the condition of remaining semi-natural habitats, which are reported to have declined over time (Williams 2006, European Environment Agency 2020). As with the loss of habitats, the drivers of degradation within some of the semi-natural habitats remains unclear.

Table 1.1 Description of Broad Habitats (Jackson 2000) explored in this thesis and the Priority Habitats associated with it (only those relevant to the thesis are considered).

Broad Habitats	Description	Priority Habitats
Acid Grassland	Characterised by vegetation dominated by grasses and herbs on a range of lime-deficient soils which have been derived from acidic bedrock or from superficial deposits such as sands and gravels. Such soils usually have a low base status, with a pH of less than 5.5.	Lowland dry acid grassland
Broadleaved, Mixed and Yew Woodland	Characterised by vegetation dominated by trees that are greater than 5 m high when mature, which form a distinct, although sometimes open canopy with a canopy cover greater than 20%. Scrub vegetation less than 5 m high requires a canopy cover greater than 30% and a patch size of at least 0.25 ha.	Lowland beech and yew woodland; Lowland mixed deciduous woodland; Wet woodland
Calcareous Grassland	Characterised by vegetation dominated by grasses and herbs on shallow, well-drained soils which are rich in bases (principally calcium carbonate) formed by the weathering of chalk and other types of limestone or base-rich rock. Soil pH tends to be high (above 6).	Lowland calcareous grassland
Dwarf Shrub Heath	Characterised by vegetation that has greater than 25% cover of plant species from the heath family (ericoids) or dwarf gorse *Ulex minor*. It generally occurs on well-drained, nutrient-poor, acid soils, and includes both dry and wet heath types.	Lowland heathland
Fen, Marsh and Swamp	Characterised by a variety of vegetation types found on minerotrophic, permanently, seasonally or periodically waterlogged peat, peaty soils or mineral soils. Fens are peatlands which receive water and nutrients from groundwater and surface run-off, as well as from rainfall. Marsh is a general term usually used to imply waterlogged soil (specifically here fen meadows and rush-pasture communities on mineral soils and shallow peats). Swamps are characterised by tall emergent vegetation. Reedbeds (i.e. swamps dominated by stands of common reed *Phragmites australis*) are also included.	Lowland Fens; Purple moor grass and rush pasture; Reedbeds
Neutral Grassland	Characterised by vegetation dominated by grasses and herbs on a range of neutral soils usually with a pH of between 4.5 and 6.5. It includes enclosed dry hay meadows and pastures, together with a range of grasslands which are periodically inundated with water or permanently moist.	Lowland meadows

1.4. SUMMARY OF KEY KNOWLEDGE GAPS

Although there are a number of long-term studies that have examined both the loss of semi-natural habitats and drivers of vegetation change in important conservation habitats, very few of these have evaluated this change beyond two snapshots in time. Consequently, the current knowledge on these drivers of change, their spatio-temporal patterns and the resulting responses are deficient. Furthermore, few studies have evaluated this change across multiple habitats within a landscape. This information is essential for understanding and comparing trajectories and mechanisms of change in different ecosystems. This can help predict future change and plan potential ameliorative actions, such as restoration.

A consensus about the prevalence of extinctions debts is hindered by different methods employed in the literature and a lack of comparison between these within the same study system. Kuussaari et al. (2009) identified this as a priority for research in their review of extinction debt, yet to date this knowledge gap remains to be addressed. This understanding is vital for developing a framework that sets out the best method for examining the existence and magnitude of extinction debt. This has important implications for conservation action and our understanding of the impacts of habitat loss and degradation.

1.5. THE STUDY SYSTEM

This thesis aims to address the knowledge gaps summarised in the previous section using southern England, in particular Dorset, Wiltshire and Hampshire, as a case study. Southern England was selected as the study system for several reasons. Firstly, southern England is a pre-dominantly lowland rural landscape, with findings being representative of many western European landscapes (Hooftman et al. 2016). Similarly, like Western Europe, southern England has experienced dramatic intensification of land use during the 20th century (Hooftman and Bullock 2012), making it an ideal case study to examine habitat loss and degradation over time. Furthermore, the study system contains a wide range of important conservation habitats including heathland, broadleaved woodland and semi-natural grasslands, in which the mechanisms of loss and degradation can be explored and compared. This is particularly relevant for calcareous grassland, since some of the largest remaining sites of this habitat type across Western Europe are located in the south of England (Toynton and Ash 2002, Redhead et al. 2019). Finally, the availability of spatial and temporal datasets offers a unique opportunity to address the knowledge gaps outlined in the previous section. Although this is true for much of the UK, in southern England, specifically Dorset, we are very fortunate to have a wealth of additional environmental datasets, including the famous Ronald Good vegetation survey undertaken in the 1930s (Good 1937), which is utilised within three of my chapters.

1.6. THESIS AIMS AND STRUCTURE

This thesis aims to examine the long-term drivers of habitat loss and quality in southern England over multiple time periods for a range of semi-natural habitats. The research questions to address this aim are:

(i) What are the spatio-temporal patterns and drivers of habitat loss? (Chapter 2 and 3)

(ii) Does habitat loss lead to extinction debts across a range of habitat types? (Chapter 4)

(iii) What are the temporal patterns and drivers of vegetation change in calcareous grasslands? (Chapter 5 and 6)

The early chapters focus on the extent and loss of habitats and therefore consider all semi-natural habitat types found across Dorset (Figure 1.1). This allows for patterns and drivers to be compared across multiple habitats. Chapter 4 explores habitat loss further by examining extinction debts in three of the semi-natural habitats considered in the previous chapters; calcareous grassland, heathland and broadleaved woodland. Although the choice of these three habitats was governed by the availability of current species data, they also represent habitats that have undergone different levels of degradation over time. Chapters 5 and 6 delve in further by focusing on the long-term drivers of habitat quality rather than overall loss. To do this in the detail required, I used calcareous grassland as a case study habitat. Calcareous grassland was selected as it is an important conservation habitat that has undergone significant declines in extent and quality over time. Furthermore, the impact of drivers such as nitrogen deposition remain unclear compared with other semi-natural habitats, hence an important knowledge gap is addressed.

The focus throughout this thesis was to use long-term data across multiple time periods. However, the availability of such data across different habitats (Figure 1.1) and locations was variable, and thus the temporal scope evaluated within each chapter is different (Figure 1.2). Chapters 2-4 focus on habitat change in Dorset, so have similar time periods evaluated (Figure 1.2). This is governed by the data available to create a time-series of habitat change including, vegetation surveys (1930 and 1980), historical Ordnance Survey maps (1950) and contemporary spatial data (1990 and 2015). Chapters 5 and 6 examine vegetation change on calcareous grassland at two different National Nature Reserves (NNR) in southern England. The time periods examined within these chapters are driven by the availability of past vegetation surveys. Chapter 5 only evaluates three time periods, the least of all the chapters (Figure 1.2), however the vegetation survey comprises a detailed transect study. Chapter 6 on the other hand, evaluates the greatest number of time periods using quadrat data from across the NNR, which has been recorded inconsistently through time. The following discussion outlines how the subsequent chapters aim to address the three research questions and the knowledge gaps summarised in section 1.4. The specific hypotheses and research questions are identified within each individual chapter.

Chapter 2 examines the patterns and drivers of change in semi-natural habitats across Dorset between 1930 and 2015. I use a variety of data sources including survey data, historical Ordnance Survey maps, resurveys and contemporary spatial layers to determine the habitat type in over 3700 sites across Dorset in 1930, 1950, 1980, 1990 and 2015. I use the generated habitat time-series dataset to explore the drivers and temporal patterns in semi-natural habitat loss over time. This directly addresses the first research question and the knowledge gap of assessing patterns of change using more than two snapshots in time.

Chapter 3 builds on the preceding chapter by modelling historical land-use/land-cover (LULC) change across the whole of Dorset between 1930 and 2015. I use existing LULC maps at two time points for 1930 (Hooftman and Bullock 2012) and 2015 (Rowland et al. 2017), along with the habitat time-series dataset produced in Chapter 2, to construct two historical LULC maps for Dorset in 1950 and 1980, which could therefore form a four-step time-series. I evaluate the accuracy and uncertainty associated with the generated maps, and use these to examine the spatial and temporal changes in semi-natural habitats over time in Dorset. This further addresses the knowledge gap relating to understanding change across multiple time periods, as with the previous chapter, but expands on this by assessing change spatially across a whole landscape.

Chapter 4 addresses the second research question by comparing three species-area relationship methods used to detect the presence of extinction debts. This is undertaken for plant communities in three semi-natural habitats across Dorset; calcareous grassland, heathland and broadleaved woodland. I use past (1930s) and present (2010s) species richness and landscape data from the preceding chapters, alongside intermediate landscape data for 1950 and 1980 (Chapter 3), where the method allows. This is the first time three extinction debt methodologies have been compared within the same landscape, thus addressing the priority for research as identified by Kuussaari et al. (2009).

Chapter 5 focuses on an important conservation habitat in southern England; calcareous grassland. I undertake a re-survey of a transect study in 2016 which was set up at Parsonage Down NNR, Wiltshire, by T. Wells in 1970 and surveyed again in 1990. I use the vegetation and soil data collected at three time points to examine vegetation change over time and the potential drivers of this, therefore addressing the third research question and the knowledge gap outlined in section 1.4. The addition of the soil data also allows for complex drivers such as nitrogen deposition to be evaluated, where the impact of this driver on calcareous grassland is uncertain.

Chapter 6 compliments the preceding chapter by examining long-term vegetation change in calcareous grassland, alongside detailed grazing records over multiple time periods. I use existing vegetation and grazing datasets, which have been collected by reserve managers between 1978 and 2010 at Martin Down NNR, located on the edge of Wilshire, Hampshire and Dorset, southern England.

Chapter 7 discusses the implications of the findings from the previous five chapters within a wider context. I critically evaluate the research undertaken, discuss novel contributions and explore future recommendations.

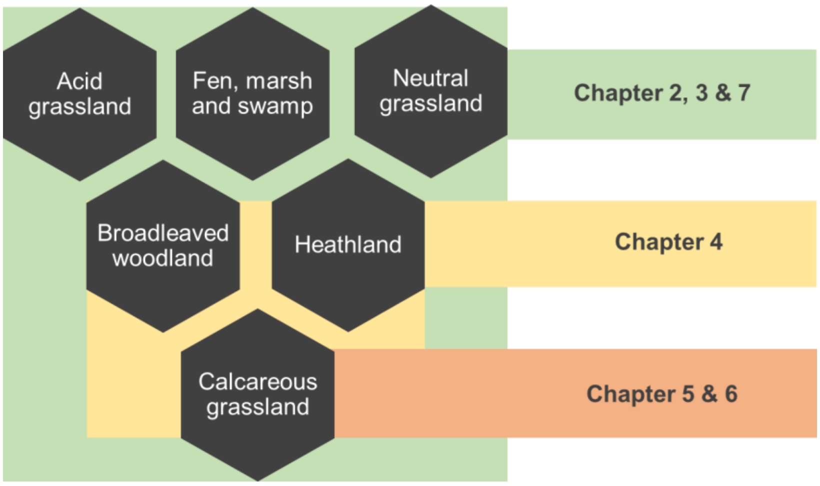

Figure 1.1 Infographic demonstrating which of the semi-natural habitats are considered within each chapter of this thesis.

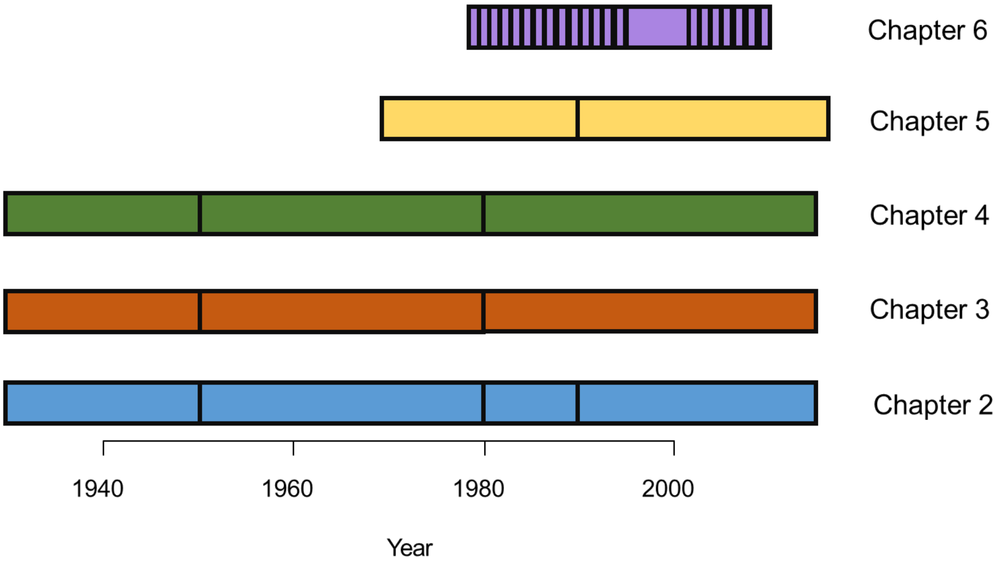

Figure 1.2 The time periods examined within each data chapter in this thesis. The black lines separating each bar indicate the time period evaluated. For example for Chapter 2, the years 1930, 1950, 1980, 1990 and 2015 were considered.

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CHAPTER 2

Ongoing, but slowing, habitat loss in a rural landscape over 85 years

2.1. ABSTRACT

Studies evaluating biodiversity loss and altered ecosystem services have tended to examine changes over the last 40 years, despite the fact that land use change and its negative impacts have been occurring over a much longer period. Examining past land use change, particularly over the long-term and multiple time periods, is essential for understanding how rates and drivers of change have varied historically. This study determined the habitat cover at over 3700 sites across the county of Dorset, southern England in 1930, 1950, 1980, 1990 and 2015, using historical vegetation surveys, re-surveys, historical maps and other contemporary spatial data. Considerable declines in semi-natural habitats occurred across Dorset between 1930 and 2015. This trend was non-linear for the majority of semi-natural habitats, with the greatest losses occurring between 1950 and 1980. This period coincides with the largest gains to arable and improved grassland, reflecting agricultural expansion after the Second World War. Although the loss of semi-natural habitats declined after this period, largely because there were very few sites left to convert, there were still a number of habitats lost within the last 25 years. These findings illustrate a long history of habitat loss in the UK, and are important for planning land management and ameliorative actions, such as restoration. My analysis also highlights the role of statutory protection in retaining semi-natural habitats, suggesting the need for continued protection of important habitats.

2.2. INTRODUCTION

Land use change is one of the main ongoing drivers of terrestrial biodiversity loss and the alteration of ecosystem functions and services (Bateman et al. 2013, Tittensor et al. 2014). Many studies evaluating biodiversity loss and altered ecosystem services have tended to examine changes over the last few decades (van Swaay et al. 2013, Renard et al. 2015, Hallmann et al. 2017, Song et al. 2018, Van der Sluis et al. 2019), despite the fact that land use change and its negative impacts have been occurring over a much longer period in Europe (Hooftman and Bullock 2012), Asia (Dearing et al. 2012) and America (Drummond et al. 2017). Examining past land use change is essential for understanding the full extent of loss and altered functions, predicting future changes, and planning potential response actions, such as ecological restoration.

Semi-natural habitats have high conservation importance in many parts of the world. Semi-natural habitats are those which were created by traditional human activities and are maintained by management, such as grazing, coppicing, cutting or burning (Poschlod and Wallis de Vries 2002). In western Europe these habitats include unimproved grasslands, heathland and broadleaved woodland. Such sites often support a high diversity of species, some of which are of conservation concern (Webb et al. 2010). Semi-natural habitats are also important for the delivery of ecosystem services including pollination, timber production, carbon storage and aesthetic value (Quine et al. 2011, Cordingley et al. 2015, Bengtsson et al. 2019). However, there has been a significant decline in many semi-natural habitats across Europe in the last century. For example, lowland heathland in Europe previously extended over several million hectares, with only an estimated 350,000 hectares now remaining (Diemont et al. 1996). Similarly, in England and Wales, an estimated 97% of semi-natural grassland was lost between 1932 and 1984 (Fuller 1987). The decline in semi-natural habitats over the past few decades is often treated as linear; but this has not been directly quantified in the UK. Furthermore, trends are presumed to be common across all semi-natural habitat types (Hooftman and Bullock 2012), though very few studies have examined the potential differences across landscapes.

In considering change in semi-natural habitats over time, whilst a linear decrease might be assumed, changes could accelerate or decelerate over time, or show more idiosyncratic patterns (Bürgi et al. 2004). Knowledge of how trends have changed in the recent past is at the core of biodiversity reporting, both nationally (DEFRA 2018) and internationally (Secretariat of the Convention on Biological Diversity 2014), but little is known about patterns over long timescales. Such information would show whether loss is slowing or increasing and even if there have been gains at any point. Trends across different habitat types could be assessed and drivers identified at different time points. Furthermore, understanding patterns of change and how drivers of decline vary in importance can be used to predict future changes, reduce ongoing habitat loss and identify where restoration could be targeted. A number of studies have assessed loss for particular habitat types over long time periods. For example, the status of the heathlands in the county of Dorset, England has been assessed since the 19th century (Moore 1962, Rose et al. 2000). Others have examined multiple habitats or land-use change using two snapshots in time (Coleman 1979, Ridding et al. 2015). But there are few studies which have assessed change in all habitats across large regional landscapes at multiple time points. An exception to this is the Countryside Survey which has assessed the extent and condition of broad habitats in the UK using 1km survey squares at discrete intervals since 1978 (Barr et al. 1993, Carey et al. 2008).

In the UK, as elsewhere in western Europe, the decline in semi-natural habitats in recent decades has been attributed to three major types of land use change; agricultural intensification, urban development and afforestation (Watson and Albon 2011). These three major land use changes increased rapidly after the Second World War, at the start of the period known as the “Great Acceleration”, when the impact of human activity on the state and functioning of the Earth System increased significantly (Steffen et al. 2007, 2015). Agricultural intensification accelerated in the 1940s due to the Agriculture Act of 1947 (Best and Coppock 1962). This continued following the UK’s accession to the European Union (EU) in 1973, causing semi-natural grasslands and heathlands to be converted to arable or fertilised for grass production. Over the same period, semi-natural habitats were also being lost to conifer plantations, due to the importance of economic forestry resulting from a Treasury policy review in 1957 (Aldhous 1997). This continued until the 1980s, when policy changes promoted planting of deciduous trees (Nail 2008). Urbanisation has also increased over the last sixty years. In the UK urban growth during the 1950s was greatest in the most urbanised regions (Parry et al. 1992). However in the latter half of the twentieth century urban sprawl increased as richer people moved away from urban centres, which led to a greater loss of countryside (Zhang 2016). Although the three major land use changes which have led to the loss of semi-natural habitats in the UK are known, few have examined the trends over time using long-term land cover data.

As elsewhere in the world, a number of policies and laws have been developed in the UK in an attempt to reduce further losses of semi-natural habitats. These range from European-wide legislations to local planning policies which aim to prevent damaging activities. European protected sites include Special Protection Areas for birds and Special Areas of Conservation. Sites that are nationally important in the UK for their flora, fauna, or geological or physiographical features are protected by law as Sites of Special Scientific Interest (SSSIs, or Areas of Special Scientific Interest, ASSIs, in Northern Ireland) (JNCC 2015). All sites protected by European and national legislation must be considered in the UK planning process. The National Planning Policy Framework sets out government's planning policies for England which requires that local authorities must ensure that any developments have minimal impact on biodiversity. Although the importance of protected areas for biological conservation is acknowledged, there is little empirical evidence of their effectiveness (Gaston et al. 2008, Greve et al. 2011). Given the importance placed on protected areas, it is important to understand if they are effective in preventing or slowing habitat loss.

Dorset is a pre-dominantly rural county in southern England (Figure 2.1), which like many other regions across Europe experienced dramatic intensification of land use during the last century. In addition, a large survey of habitats was carried out during the 1930s, which presents a unique historical baseline. This makes Dorset an ideal case study to examine habitat change over time, with findings being representative of many western European lowland landscapes (Hooftman et al. 2016). In this paper I quantify changes in semi-natural habitats across the Dorset landscape at five time points between 1930 and 2015, using survey data and contemporary spatial datasets in GIS. Based on the evidence reviewed above I aim to address the following questions;

(i) Has the loss of semi-natural habitats been linear over time?

(ii) What are the main drivers of loss for each semi-natural habitat, and do these change over time?

(iii) Do protected sites have lower rates of change than other areas of semi-natural habitat?

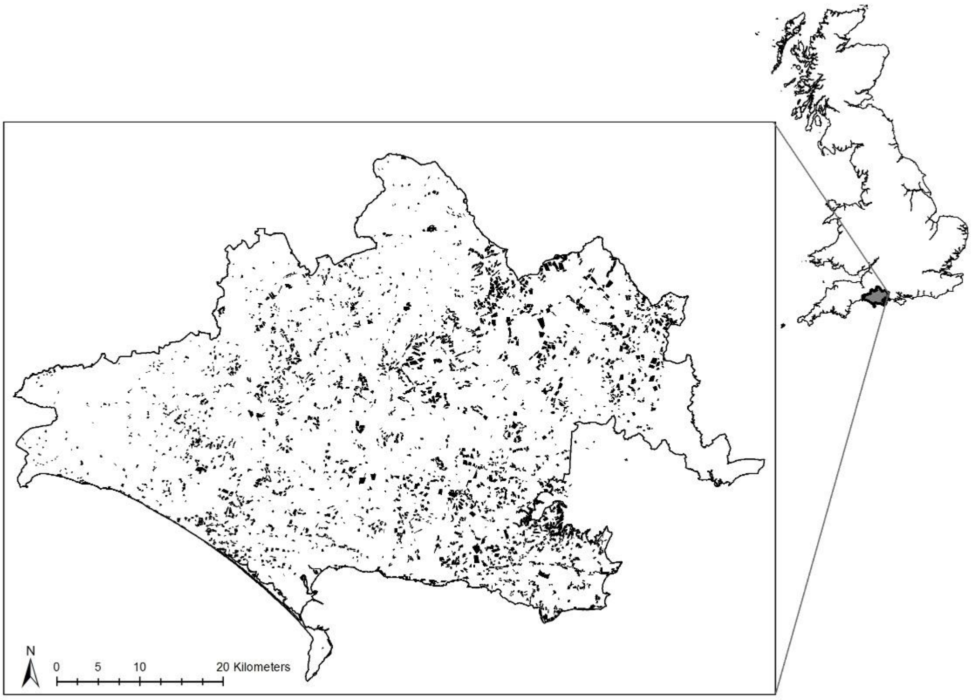


Figure 2.1 Location of sites within Dorset, south England. County boundary excludes the boroughs of Poole and Bournemouth, which were not part of Dorset in the 1930s.

2.3. METHODS

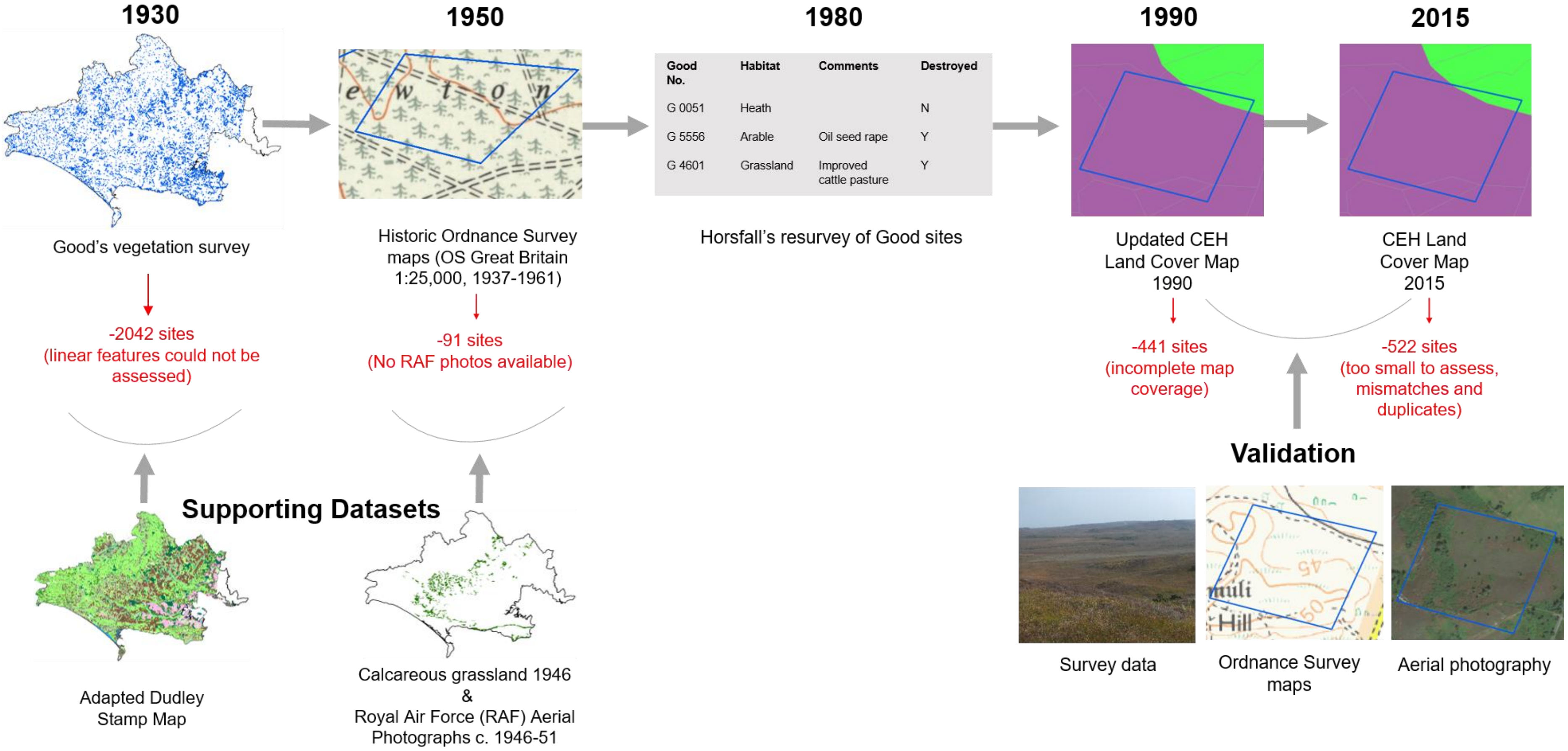
To quantify changes in semi-natural habitats across Dorset over time, I generated a time series of habitat/land cover for 1930, 1950, 1980, 1990 and 2015 (Figure 2.2). The starting point for the time series used Ronald Good's vegetation survey undertaken between 1931 and 1936. Good undertook a systematic survey of vascular plant species using the 'stand' method (see Good, 1937) at 7575 sites across Dorset (referred to subsequently as "Good sites") with the aim of producing distribution maps for single species. Stands were '…reasonably distinct topographical and ecological entit[ies]…' and were required to be '…as evenly scattered as possible' across Dorset with an average of 5-6 stands per square mile (Good, 1937, p115). The "Good sites" were recorded on a series of six-inch to the mile (1:10,560) Ordnance Survey (OS) maps which were later digitized by the Dorset Environmental Records Centre (DERC), along with site and species information, which included a species list of all vascular plants encountered whilst Good traversed each site. Sites varied in size, ranging from ca. 0.5 to 70 ha. In the 1980s, 6880 of these sites were revisited by Anne Horsfall, who simply determined whether the original habitat remained or not. These 6880 Good sites where the habitat type was known for the two time points were used alongside historical OS maps and contemporary land cover spatial layers to construct a habitat time series (Figure 2.2).

2.3.1. Habitat extent in the 1930s

DERC allocated a broad habitat type to each site based on the descriptions provided in Good's diaries (Good 1937), which are closely aligned to those defined by Jackson (2000) for UK habitat types in general (Table 2.1, first column). I used two other datasets to validate the assigned broad habitat type for the 1930s. Firstly, I intersected the sites with the adapted Dudley Stamp Map created by Hooftman and Bullock (2012) in ArcGIS v10.4 (© ESRI, Redlands, CA). The Dudley Stamp Map was created from the 1930s Land Utilisation Survey of Britain, where volunteers mapped land-use on OS maps (Stamp 1931). Secondly, I ran Good's plant species records for each site through TABLEFIT (Hill 1996), to determine the National Vegetation Classification (NVC) community. The NVC classifies the plant communities of Britain (Rodwell 1992). Using the classification table in Ridding et al. (2015), I assigned the NVC community for each site to one of the broad habitats detailed in Table 2.1. Over 75% of sites were assigned a broad habitat which was consistent across two or three of the datasets (Good description, Dudley Stamp Map, NVC community). For the remaining sites whose habitat classification differed across the three datasets, I used the Good description to designate the habitat type, since these direct survey data are likely to be more reliable than the other two datasets. I removed all sites which were designated as "hedgerows" in the 1930s, since these sites were too small to assess accurately in the later time periods (n = 2042) as the Land Cover Maps (see below) do not map linear or boundary features (Figure 2.2).

2.3.2. Habitat extent in the 1950s

For sites which had remained the same habitat in 1980 (determined by Horsfall) as in the 1930s, I assumed the same habitat in the 1950s (3892 sites). For the remainder, I utilised the OS Great Britain 1:25,000, 1937-1961 (Ordnance Survey 1961) map series to determine the habitat cover during the 1950s. This OS series comprised 10 kilometre squares across Great Britain, and most of the individual 10 kilometre square maps including Dorset were completed around the 1950s. Since the OS maps displayed particular symbols for certain habitats (see Figure 2.2) I could distinguish the main habitat for most sites (coniferous and broadleaved woodland, water, urban, heath, marsh and grassland), which I classified according to the broad habitat types (Table 2.1). For some sites that were semi-natural grassland in the 1930s, no markings were present on the 1950s OS map to indicate the habitat type. I used a GIS layer of calcareous grassland habitat in 1946 created by DERC using a variety of sources including Royal Air Force (RAF) Aerial Photographs c. 1946-51, OS maps and The Conservation of Chalk Downland in Dorset, 1973 (see Edwards, 2006), to indicate which sites were still calcareous grassland. The remaining unclassified sites which were semi-natural grassland in 1930 (n = 550), were thus likely to be either arable, improved grassland or another type of semi-natural grassland. To distinguish these, I utilised RAF Aerial Photographs c.1946-51 (Dorset County Council 2018). Arable fields were open with furrows, interpreted as a sign of ploughing, whilst pastures were open without furrows, often with grazing animals present. Darker colours and "rough patches" were used to distinguish between unimproved and improved grassland. This technique was very time-consuming, so was only employed where other methods failed to identify the habitat. Aerial photographs were unavailable for 91 sites, and so these were removed from further analysis. Where the 1930s habitat had clearly been lost, but the OS map did not give any indications as to the current habitat, I assigned the habitat present in the 1980s.



Good No.	Habitat	Comments	Destroyed
G 0051	Heath		N
G 5556	Arable	Oil seed rape	Y
G 4601	Grassland	Improved cattle pasture	Y

Figure 2.2 The methodology used to determine habitat cover within each Good site for 1930 (Good 1937), 1950 (Ordnance Survey 1961), 1980 (Horsfall 1981), 1990 (Rowland et al. 2017b) and 2015 (Rowland et al. 2017a), with the validation datasets (Ordnance Survey (2017), © ESRI World Imagery), supporting datasets (Adapted Dudley Stamp Map re-created from Hooftman and Bullock (2012), calcareous grassland map re-created from DERC data) and the number of sites removed from each stage in the analysis.

Table 2.1 Broad habitat classifications for 1930, 1950 and 1980, matched with categories from the Land Cover Map 2015, alongside the final combined habitat classification for the whole time series. Bracken is not mapped in the LCMs, as the consistency cannot be guaranteed across the country (Rowland et al. 2017a); therefore it is often associated with the other broad habitat types. It was also impossible to detect sites which were solely bracken in the 1950s using the OS maps, so these sites were grouped under a “Mosaic” category. I grouped “Littoral Sediment”, “Littoral Rock”, “Supra-littoral Sediment”, “Supra-littoral Rock” categories used in the LCMs into a “Coastal” category, because for some sites the habitat switched between two of these coastal types in the two LCMs, which likely reflects classification issues rather than habitat change.

Broad Habitat (1930, 1950, 1980)	**Land Cover Map Habitat (1990, 2015)**	**Combined Time-Series Habitat Classification**
Rivers and streams	Freshwater	Water
Standing open water and canals		
Bracken (excluding 1950)	N/A	Mosaic
Arable and horticulture	Arable and horticulture	Arable and horticulture
Bog	Bog	N/A (not found in Dorset)
Fen, marsh and swamp	Fen, marsh and swamp	Fen, marsh and swamp
Acid grassland	Acid grassland	Acid grassland
Calcareous grassland	Calcareous grassland	Calcareous grassland
Neutral grassland	Neutral grassland	Neutral grassland
Improved grassland	Improved grassland	Improved grassland
Heathland	Dwarf Shrub Heath	Heathland
Boundary and linear feature	N/A	N/A (Removed these sites)
Inland rock	Inland rock	Inland rock
N/A	Saltwater	Coastal
Littoral rock	Littoral rock	
Littoral sediment	Littoral sediment	
Supra-littoral rock	Supra-littoral rock	
Supra-littoral sediment	Supra-littoral sediment	
Built-up areas and gardens	Urban	Urban
	Suburban	
Broadleaved woodland	Broadleaved, mixed and yew woodland	Broadleaved, mixed and yew woodland
Coniferous woodland	Coniferous woodland	Coniferous woodland

2.3.3. Habitat extent in the 1980s

Sites were revisited by Anne Horsfall in the 1980s (see Horsfall, 1981). Using Good's plant list for each site, Horsfall determined whether the habitat reported in the 1930s remained or had changed. She recorded the general habitat alongside additional notes, which I used to classify each site into a broad habitat type (Table 2.1). I made some assumptions during the classification process in order to assign woodland sites to coniferous or broadleaved woodland. For most sites where plantations were present in the 1980s, Horsfall had made additional notes allowing me to determine whether the plantation was broadleaved, coniferous or mixed. For a small number of sites (<10) Horsfall provided no information, and I assumed a coniferous plantation since the majority of British tree planting in the mid twentieth century was coniferous (Mason 2007). I also assigned as improved grassland all the sites which Horsfall described as pastures. For the majority of sites, this was confirmed by notes provided by Horsfall (Figure 2.2).

2.3.4. Habitat extent in 1990 and 2015

To determine the habitat at each site in 1990, I used an updated dataset of the UK Land Cover Map 1990 (LCM1990) (Rowland et al. 2017b). The original LCM1990 (Fuller et al. 1993), is not directly comparable with Land Cover Map 2015 (LCM2015) (Rowland et al. 2017a) because it uses different land cover classes and has a different spatial structure. To make it comparable with LCM2015, the updated 1990 Land Cover dataset (Rowland et al. 2017b), was created using the same methodology as that used to create the LCM2015. Using ArcGIS on the revised LCM1990, I assigned the habitat for each site as that with the largest percentage cover in the site. Since the updated LCM1990 does not yet have full coverage across Dorset, 441 sites could not be assessed and were removed from the study (Figure 2.2). I used the same methodology with LCM2015 to identify the main habitat type for each site in 2015.

2.3.5. Combining habitat time series data

Habitat data for the 1930s, 1950s, 1980s, 1990s and 2015 were standardised using Table 2.1. The habitat classifications from the 1930s, 1950s, 1980s and the LCMs were largely similar, as they were all based on Jackson (2000) broad habitat categories. I generated transition matrices between each time period, with partially converted sites being classified as lost. This highlighted any apparent habitat changes that were unlikely to occur in reality, for example acid grassland converting to calcareous grassland. Where unlikely conversions were identified in 1990 (where both 1980 and 2015 remained consistent), I checked aerial photography for the closest time period available, 2002 (Dorset County Council 2018). This resolved issues for a number of urban sites, which were identified as improved grassland in the LCMs due to large gardens with extensive lawns. This left a total of 3784 sites for analysis, where the broad habitat was known in each time period. Since the methodology I used for classifying habitats in the latter periods (1990 and 2015 used the Land Cover Maps), was quite different from the previous time points, I performed validation using additional datasets to assess the accuracy and consistency of the time series across all periods, which I describe in Appendix A.1.

2.3.6. Statistical analysis

To examine whether the losses of semi-natural habitats (acid grassland, broadleaved woodland, calcareous grassland, fen, marsh and swamp, heathland and neutral grassland) were linear over time, I constructed general linear models (GLMs) and generalized additive models (GAMs), with year as the dependent variable. GAMs are often used to detect non-linearity in time-series data (Granadeiro et al. 2004, Watson et al. 2018). Where the AIC difference between the GLM and GAM was less than 2, I took this as providing evidence for little difference between the models (Burnham and Anderson 2002), and so the GAM model was rejected and I concluded the pattern was linear. Where this was not the case, I included year as a smoother term in the GAM model using the “mgcv” package (Wood 2017) in R v3.0.2 (R Core Team 2019).

For each time period, I identified those sites in which the habitat type changed and used Chi-squared tests to examine whether new habitat types fitted a null hypothesis of a random distribution of different types. Separate Chi-squared tests were performed according to the original habitat type; neutral grassland, calcareous grassland, fen, marsh and swamp, heathland and acid grassland. When assessing what habitats changed into, those with a low coverage were combined into an “other” category (coastal, water, fen, marsh, swamp, acid grassland, calcareous grassland, heathland, mosaic and inland rock) for this analysis. Where the assumptions required for a Chi-squared test were not met, I used Fisher’s exact test for small sample sizes.

Protected sites were determined using the digital boundary data for SSSIs in ArcGIS (Natural England 2014). SSSIs were first established in the 1950s, but were later re-notified under the Wildlife and Countryside Act 1981, with sites still being added until present, but to a much lesser extent (see Ridding et al., 2015). SSSIs were chosen to represent protected areas in the UK since this system provides the underpinning statutory protection for all sites, including those which are of European importance. Sites were classified as protected if at least 90% of their area fell within the SSSI boundary, which accounted for small differences in the borders of both datasets. I then calculated the turnover at each site, with turnover defined as the number of time periods in which the habitat changed (Swetnam 2007). To examine whether protected sites were more likely to have no turnover, I used a Chi-squared test to determine if the number of sites with no habitat turnover fitted a null hypothesis of equal distribution between protected and unprotected sites. Individual tests were performed according to the original 1930s habitat of the site: acid grassland, calcareous grassland, fen, marsh and swamp, heathland and neutral grassland.

2.4. RESULTS

2.4.1. Trends in semi-natural habitats

There were considerable losses across the majority of semi-natural habitat sites examined – including acid grassland, calcareous grassland, fen, marsh and swamp, heathland and neutral grassland, – in Dorset between 1930 and 2015 (Figure 2.3). Of the 3146 semi-natural habitat sites assessed, 62% of sites remained as their original habitat in 2015. The greatest losses were found for neutral grassland, with 97% of sites lost between across the Dorset landscape between 1930 and 2015, followed by a loss of 70% for calcareous grassland. Broadleaved woodland remained fairly consistent with a slight linear increase overall (3%), though it did experience declines between 1930 and 1980. The majority of the declining semi-natural habitats, including acid grassland, calcareous grassland, heathland and neutral grassland, decreased non-linearly over time (Table 2.2). The greatest declines occurred between

1930 and 1980, with the highest losses occurring between 1950 and 1980, after which the loss of sites appeared to level-off for some habitats. Fen, marsh and swamp habitats were the only semi-natural habitat type to decline linearly between 1930 and 2015 (Table 2.2).

2.4.2. Timing of habitat conversion

Intensive land cover types within the landscape including coniferous woodland, improved grassland, arable and urban areas increased rapidly, at the expense of semi-natural habitat sites, largely between 1930 and 1980 (Figure 2.3). The greatest increase in the number of improved grassland and arable sites occurred between 1950 and 1980, which corresponds to the period with the highest percentage loss of semi-natural habitat sites (-20%). For urban and coniferous woodland, the greatest gains were between 1930 and 1950. After 1980 the number of sites converted to the intensive land covers decreased (Figure 2.3). This was particularly clear for arable, coniferous woodland and urban, which showed non-linear trends (Table 2.2) and evidence of levelling off in the later time period, with some arable sites even being lost between 1990 and 2015. Improved grassland, on the other hand, increased linearly throughout the survey period.

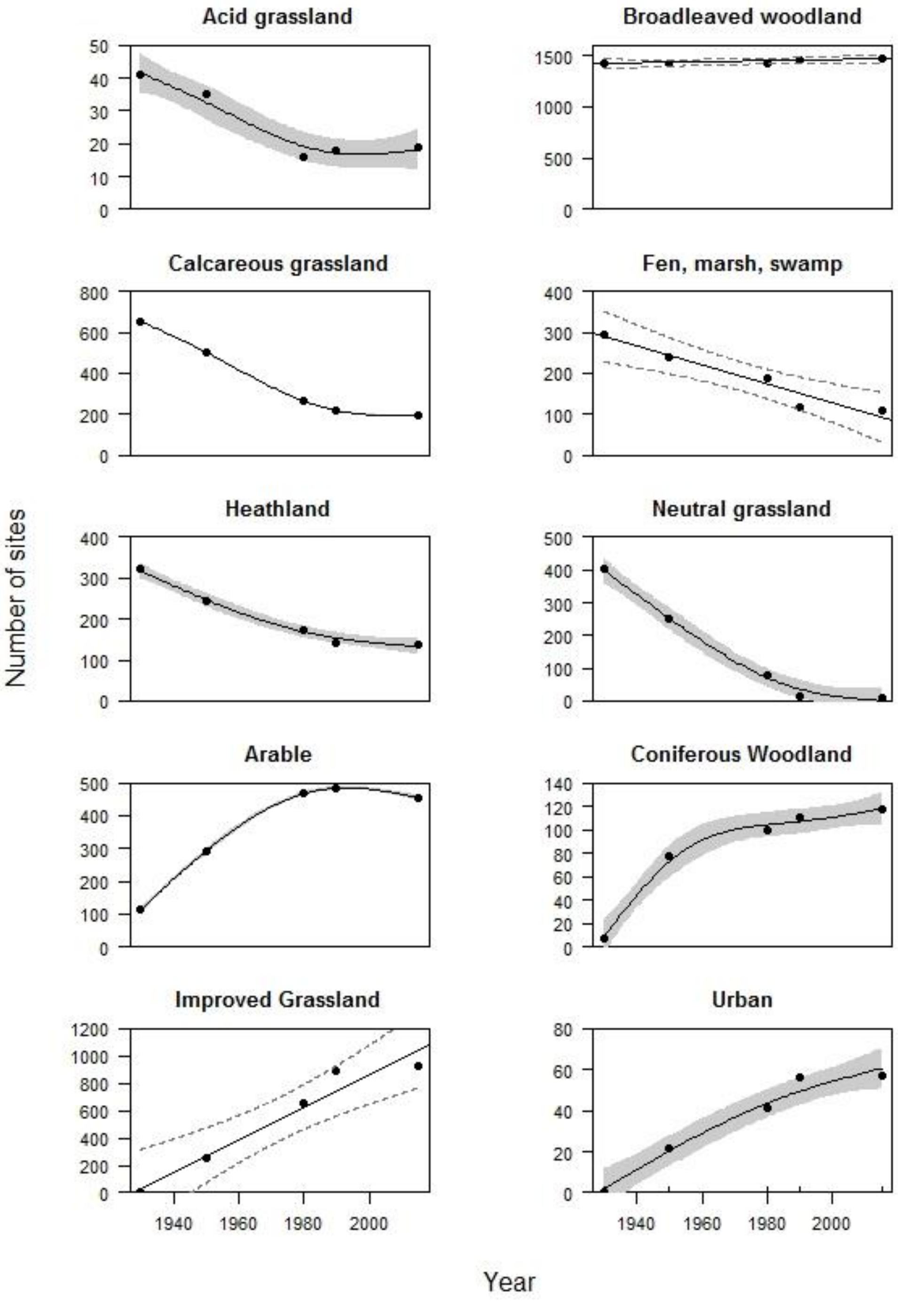


Figure 2.3 The number of sites for each semi-natural habitat (acid grassland, broadleaved woodland, calcareous grassland, fen, marsh and swamp, heathland, neutral grassland) and intensive land use type (arable, coniferous woodland, improved grassland, urban) across Dorset in 1930, 1950, 1980, 1990 and 2010. Trend lines with 95% confidence intervals indicated in grey, represent the fitted general linear models for improved grassland, broadleaved woodland and fen, marsh and swamp, and the generalized additive models for acid grassland, calcareous grassland, heathland, neutral grassland, arable, coniferous woodland and urban.

2.4.3. Drivers of change for semi-natural habitats

The types of land cover to which semi-natural sites were converted to differed significantly across the landscape among neutral grassland, calcareous grassland, fen, marsh and swamp, heathland and acid grassland sites in 1950, 1980, 1990 and 2015 (Table 2.3). Considerable proportions of semi-natural habitat were lost to arable before 1980 (Figure 2.4), particularly calcareous and neutral grassland, with only small proportions from acid grassland, fen, marsh and swamp, and heathland. Large percentages of semi-natural habitat were also converted to improved grassland, where in 1980 at least 45% of each of the semi-natural habitats had been lost to improved grassland. The proportions increased further in 1990 and 2015 for neutral, acid and calcareous grassland, where in 1990 and 2015 conversion to improved grassland accounted fully for the loss of acid grassland and neutral grassland respectively. A number of fen, marsh and swamp, and heathland habitats were converted to broadleaved woodland, possibly due to scrub encroachment. Coniferous woodland was responsible for the majority of heathland loss in 1950, 1990 and 2015, with some conversion of heathland to improved grassland and smaller proportions being lost to broadleaved woodland and urban areas (Figure 2.4).

2.4.4. Land cover change in protected sites

The majority of sites which were protected via designation as a SSSI had 0 turnover (75%), meaning the semi-natural habitat classified for 1930 remained between 1950 (post designation) and 2015 (Figure 2.5). Turnover was greater in the non-protected sites (only 31% had 0 turnover), with the majority of sites having at least one habitat change. This was the case for calcareous grassland ($X^2 = 9.93$, $df = 1$, $p = 0.002$), acid grassland ($X^2 = 24.06$, $df = 1$, $p < 0.001$), heathland ($X^2 = 5.74$, $df = 1$, $p = 0.017$) and fen, marsh and swamp ($X^2 = 4.70$, $df = 1$, $p = 0.030$), though protection did not affect the retention of neutral grassland between 1950 and 2015 ($X^2 = 1.03$, $df = 1$, $p = 0.310$).

Table 2.2 GLM and GAM results including AIC, R^2 and smoother term values (edf = estimated degrees of freedom) (for latter only) used to examine whether trends in semi-natural habitat (acid grassland, broadleaved woodland, calcareous grassland, fen, marsh and swamp, heathland, neutral grassland) and land cover (arable, coniferous woodland, improved grassland, urban) were non-linear between 1930 and 2015 in Dorset.

	GAM					**GLM**	
Habitat/land cover	**AIC**	**R^2**	***p***	**F**	**edf**	**AIC**	**R^2**
Acid grassland	29.16	0.92	0.079	17.61	2.32	35.68	0.72
Broadleaved woodland	45.06	0.60	0.196	3.01	1.59	46.79	0.42
Calcareous grassland	23.25	1	0.002	13169	3.00	59.44	0.90
Fen, marsh, swamp	49.70	0.91	0.007	39.12	1	49.70	0.91
Heathland	41.13	0.98	0.018	80.12	2.24	50.57	0.88
Neutral grassland	47.73	0.99	0.020	96.59	2.37	58.36	0.88
Arable	34.40	0.99	<0.001	1770	1.99	61.88	0.73
Coniferous woodland	36.66	0.97	0.075	47.53	2.81	48.51	0.76
Improved grassland	62.34	0.95	0.018	38.87	1.81	64.83	0.92
Urban	34.93	0.95	0.020	33.72	1.76	37.88	0.93

Table 2.3 Chi-square test results for examining whether current land cover across lost habitat sites were randomly distributed for acid grassland, calcareous grassland, fen, marsh and swamp (FMS), heathland and neutral grassland across the four time periods; 1950, 1980, 1990 and 2015 in Dorset. Where assumptions required for a Chi-squared test were not met (X^2 = -), Fisher's exact results are presented.

	1950			1980			1990			2015		
	X^2	*df*	*p*	X^2	*df*	*p*	X^2	*df*	*p*	X^2	*df*	*p*
Acid	-	-	<0.001	68.24	5	<0.001	-	-	<0.001	-	-	<0.001
Calcareous	63.78	5	<0.001	77.68	5	<0.001	73.48	5	<0.001	68.10	5	<0.001
FMS	24.90	5	<0.001	48.58	5	<0.001	57.21	5	<0.001	43.85	5	<0.001
Heathland	52.09	5	<0.001	21.36	5	<0.001	14.78	5	0.010	64.29	5	<0.001
Neutral	74.41	5	<0.001	89.85	5	<0.001	72.40	5	<0.001	-	-	<0.001

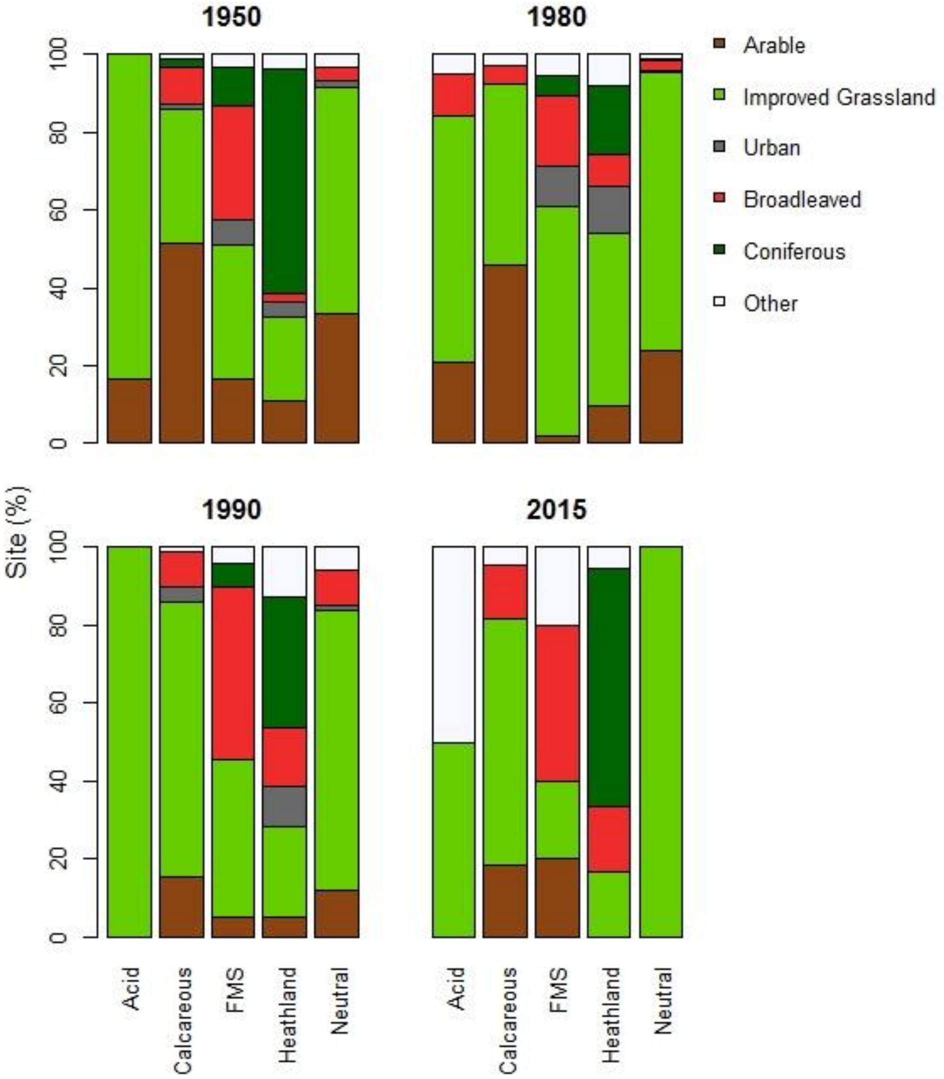


Figure 2.4 The percentage of acid grassland, calcareous grassland, fen, marsh and swamp (FMS), heathland and neutral grassland sites which converted to a more intensive land cover (arable, coniferous woodland, improved grassland, urban), broadleaved woodland and other in Dorset in 1950, 1980, 1990 and 2015.

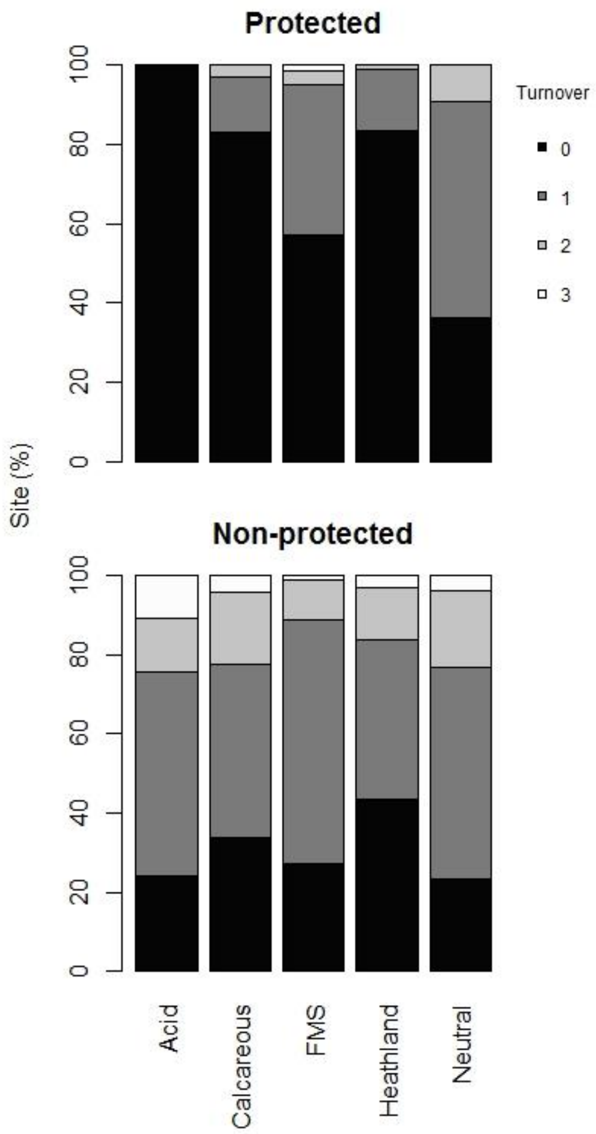


Figure 2.5 The turnover of protected and non-protected sites across Dorset between 1950 (post protection designations) and 2015 for sites which were acid grassland, calcareous grassland, fen, marsh, swamp (FMS), heathland and neutral grassland in 1930, where turnover is defined as the number of time periods in which the habitat changed (0 indicates the habitat has not changed).

2.5. DISCUSSION

I have identified changes in habitat types by assessing more than 3700 sites in the Dorset landscape between 1930 and 2015 over five consecutive time intervals. The creation of this novel dataset for Dorset's semi-natural habitats has provided a rare opportunity to examine the loss of habitats, the patterns of change and the fate of sites across multiple time periods in a region which is broadly representative of many lowland landscapes in western Europe that have a predominantly agricultural land use.

2.5.1. Trends in semi-natural habitats

I found considerable losses over 85 years for the majority of semi-natural habitats across the Dorset landscape, including neutral grassland, calcareous grassland, fen, marsh and swamp, acid grassland and heathland. This is consistent with other studies in Dorset (Rose et al. 2000, Hooftman and Bullock 2012), the UK (Fuller 1987, Ridding et al. 2015) and across Europe (van Dijk 1991, Piessens and Hermy 2006). The NCC (1984) revealed a loss of 70% of chalk grassland in Dorset between 1934 and 1972, which is the same as the loss I report between 1930 and 2015. For the majority of habitats in Dorset, the decline was non-linear between 1930 and 2015. The greatest losses occurred during 1950 and 1980, after which the decline in semi-natural habitats decreased. While this might be seen as a positive for conservation, it is mostly due to the fact that there was very little habitat left in this landscape by this period. For instance, only 12 of the original 401 neutral grassland sites remained in 2015. However, other factors including the timing of drivers (discussed below) and the designation of SSSIs and other similar protection schemes, will have increasingly prevented damaging activities on many semi-natural habitats (JNCC 2015).

The non-linear trend of habitat loss revealed in this study has important implications for the reporting of biodiversity change over time, since many long-term studies often focus on the last forty years at best. For instance, Hallmann et al. (2017) reported a 76% decline in flying insect biomass German protected areas between 1989 and 2016, whilst Powney et al. (2019) showed that one third of insect pollinator species experienced declines between 1980 and 2013 in Great Britain. Both studies evaluated species' trends after 1980, by which time the majority of semi-natural habitats were already lost in this study. Indeed, data on biodiversity loss to inform reporting to the Convention on Biological Diversity goes back to the 1970s at most in the UK (DEFRA 2018), a country with one of the longest histories of monitoring in the World (Pocock et al. 2015). There are few exceptions to this, for example Hambler et al. (2011) examined extinction debts in Britain going back to the 19th Century. This still raises the question as to what species loss occurred during the earlier period of massive habitat loss before such recording started. Indeed, the "shifting baseline syndrome" addresses the problem that a lack of understanding of historic losses may cause an acceptance of the current low biodiversity state as being normal (Soga and Gaston 2018). Furthermore, ongoing species' declines may be a delayed response to this past habitat loss, i.e. the paying of extinction debts (Sang et al. 2010). Hooftman et al. (2016) found that plant extinctions in intact habitat in Dorset were driven by declining connectivity as a result of landscape-scale habitat loss. This also suggests that even if habitat loss completed ceased, which is not yet evident in Dorset, losses in biodiversity may continue.

2.6.2. Timing of habitat conversion

Between 1930 and 2015 a number of land cover types, representing intensive land uses, increased considerably across the Dorset landscape, including arable, improved grassland, coniferous woodland and urban areas. Arable and improved grassland increased the greatest from 1950 to 1980, which suggests that habitat conversion to these land covers did not necessarily occur immediately after the Second World War and continued after the UK's accession to the EU in 1973 (Fuller 1987). The number of sites converted to arable fell after the 1980s, around the time where crop yields tripled in the UK (Pretty et al. 2000), through mechanisation and chemical application, meaning less area was required to maintain yields. Agri-environment schemes were also introduced, while a number of economic and political factors led to a reduction in the number of farms, including falls in prices for agricultural products and farm income, as well as diseases affecting cattle such as Mad Cow Disease (BSE) and Foot and Mouth (Zayed 2016).

In the period 1990-2015 the number of arable sites decreased for the first time during the study period. The European Environment Agency (EEA) found that urbanisation was predominantly occurring on arable land between 1990-2000 (European Environment Agency 2010) and 2006-2012 (European Environment

Agency 2017), but in Dorset I found no evidence of this. Instead the main change to arable sites 1990-2015 was conversion to improved grassland. This most likely reflects the agricultural system in the UK, whereby grass and clover leys are often added to arable rotations, to manage weed problems such as black grass or to increase soil fertility (AHDB 2018).

The majority of urbanisation in Dorset occurred during 1930-1950 in this study, which includes the period immediately after the Second World War. During this time no planning permission was required for land development, until the Town and Country Planning Act was established in 1947. Following this period there was a reduction in the number of sites converted to urban, despite the fact that this land cover is predicted to increase across Europe in the future (European Environment Agency 2017). This may be because Dorset is a predominantly rural county (Hooftman and Bullock 2012), where urban pressures are largely confined to the main towns of Bournemouth and Poole (Webb and Haskins 1980). None of the sites occurred in these areas, since they were not examined in the original Good survey (Good 1937).

The biggest increase in coniferous woodland in Dorset was also in the period 1930-1950. For coniferous woodland this was largely driven by the formation of the Forestry Commission in 1919 and the objective of having a strategic supply of timber which led to extensive planting until 1980 when the emphasis shifted towards sustainable forestry (Mason 2007). This mirrors the findings in this study in which a non-linear trend in afforestation is evident, with a slowing in the later periods. Afforestation was also found to be one of the most important processes for landscape change across Europe (Bürgi et al. 2017).

Although the loss of semi-natural habitats to agricultural intensification, urban development and afforestation was highest following the Second World War until the 1980s, there were considerable losses in the landscape after this period. This suggests that the three drivers of change are still a threat to biodiversity in the present day. This has important implications for conservation and landscape management in the future. Indeed, the pattern of urbanisation is currently changing in Dorset and elsewhere in England as house building is expanding into more rural areas (Campaign to Protect Rural England 2018). Agriculture could continue its gradual expansion under policies aimed at increasing food production (Reif and Vermouzek 2019) or under new post-Brexit agricultural policies. Conversely policies for a more sustainable future might facilitate expansion and restoration of semi-natural habitats, as promised under the UK Government's 25 Year Environment Plan (Isaac et al. 2018) and more widely for the UN's Sustainable Development Goals.

2.5.3. Differences among semi-natural habitats in drivers of change

There were significant differences in the drivers of loss among the different semi-natural habitats during different time periods. More calcareous grassland sites were lost to arable land after the 1940s compared with neutral grassland, acid grassland and fen, marsh and swamp. Ridding et al. (2015) found that although greater numbers of mesotrophic sites were lost throughout England between 1960 and 2013 compared with calcareous grassland, the proportion of sites which were converted to arable was greater for calcareous grassland compared with mesotrophic grassland, wet grassland and lowland heath and dry acid grassland, which is consistent with this study. Considerably fewer acid grassland and fen, marsh and swamp habitats were converted to arable compared with calcareous and neutral grassland, which is most likely due to; a) more constrained soils that are less fertile for arable agriculture; and b) the lack of advances in drainage technology until the 1980s (Green 1990).

Conversion to improved grassland was a key driver of change for most semi-natural habitats throughout the study period, particularly for acid, calcareous and neutral grassland after 1950. Some of these changes may have been due to fertiliser application or reseeding, however some changes may be attributable to more subtle processes such as nitrogen deposition or grazing management, rather than land-use change per se (Maskell et al. 2010, Diekmann et al. 2014). A re-survey of Good's calcareous grassland sites in 2009 revealed a shift from species typical of species-rich calcareous grasslands towards those more typical of mesotrophic grassland, with eutrophication and management changes suggested as potential causes (Newton et al. 2012).

During all time points, excluding 1950-1980, afforestation was the greatest driver of heathland loss. The large conversion to coniferous woodland in the 1950s corresponds to the period where conifer planting was promoted, as previously mentioned. Heathland losses to coniferous woodland in 1990 and 2015 were likely to be a result of inappropriate management. Diaz et al. (2013) conducted a re-survey of the original Good heathland sites in 2010 and also found that vegetation shifted towards a woodland community, whilst Rose et al. (2000) reported increases in scrub and woodland on heathland in between 1987 and 1996. This supports the findings of heathland also being lost to broadleaf woodland in this study, which is largely attributed to the reduction in rough grazing and controlled burning (Moore 1962). Urbanisation was also a driver of heathland loss in Dorset, which largely occurred in 1980 and 1990. This corresponds with Webb (1990) who reported a loss of 150 ha of heathland for roads, houses and factories between 1978 and 1987 and Rose et al who reported a further loss of 100 ha 1987-1996.

Although Good surveyed the Dorset landscape evenly, with roughly 5-6 stands per square mile (Good 1937), it is possible that biases were introduced into the time series when particular sites were removed from the study (see Figure 2.2). For instance, over 400 sites were eliminated from the north-west due to incomplete land cover map coverage in 1990, whilst sites which were less than 0.5 ha were also removed (Figure 2.2). While it is not clear if eliminating these sites introduced any bias, one might expect the habitat losses to be underestimated in this study, given that smaller sites (<0.5 ha), which are more vulnerable to loss, were not considered. For four of the six semi-natural habitat types I found significant differences between the size of sites which remained and were lost between 1930 and 2015, but these patterns varied. For broadleaved woodland and calcareous grassland lost sites were significantly larger than those which remained, but the opposite pattern was found for heathland and for fen, marsh and swamp (see Appendix A.2 for further details).

2.5.4. Land cover change in protected sites

Sites which are protected through designation as a SSSI were more likely to remain unchanged compared to those which are not protected. Ridding et al. (2015) also found that 91% of protected English semi-natural grasslands persisted between 1960 and 2013, compared with only 27% in non-protected sites. While there has been controversy about the effectiveness of protected areas, they have proven valuable around the world at conserving habitat (Geldmann et al. 2013). The retention of neutral grassland in this study was not affected by protection status, which may be because the management of such grasslands has caused vegetation change. For instance, only 42% of neutral grasslands which are designated as SSSIs are considered to be in favourable condition, with under-grazing and abandonment being the main cause of decline (Williams 2006). This study suggests that statutory protection is beneficial in preventing habitat loss through damaging activity, however appropriate management of protected sites is essential.

2.6. CONCLUSIONS

This study has confirmed a considerable decline in semi-natural habitats across the Dorset landscape between 1930 and 2015. This trend was non-linear for the majority of semi-natural habitats, with the greatest losses occurring between 1950 and 1980, and slowing after this time. This period coincides with the largest gains to arable and improved grassland, suggesting that these drivers did not necessarily lead to the loss of habitats immediately after the Second World War, as often presumed, but instead conversion to intensive land covers continued to increase until 1980. Although the loss of semi-natural habitats declined after this period, largely because there were very few sites left to convert, habitats were still being lost over the last 25 years. This suggests an urgent need both to protect remaining semi-natural habitats fully, which this study has shown to be effective, but also to restore these habitats to start to reverse the huge losses.

2.7. REFERENCES

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CHAPTER 3

Modelling historical landscape changes

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CHAPTER 4

Inconsistent detection of extinction debts using different methods

4.1. ABSTRACT

The extinction debt, delayed species extinctions following landscape degradation, is a widely discussed concept. But a consensus about the prevalence of extinctions debts is hindered by a multiplicity of methods and a lack of comparisons among habitats. I applied three contrasting species-area relationship methods to test for plant community extinction debts in three habitats which had different degradation histories over the last century: calcareous grassland, heathland and woodland. These methods differ in their data requirements, with the first two using information on past and current habitat area alongside current species richness, whilst the last method also requires data on past species richness. The most data-intensive, and hence arguably most reliable method, identified extinction debts across all habitats for specialist species, whilst the other methods did not. All methods detected an extinction debt in calcareous grassland, which had undergone the most severe degradation. I conclude that some methods failed to detect an extinction debt, particularly in habitats that have undergone moderate degradation. Data on past species numbers are required for the most reliable method; as such data are rare, extinction debts may be under-reported.

4.2. INTRODUCTION

Habitat destruction is one of the main drivers of biodiversity declines worldwide (Tittensor et al. 2014). Loss and fragmentation of natural and semi-natural areas reduces the habitat available to associated plant and animal species. Even within the remaining habitat patches, environmental degradation and poor connectivity can lead to ongoing species loss (Hooftman et al. 2016). Population extinction may be immediate for some species, while others can show a delayed response. In a community context, this latter phenomenon is known as extinction debt, whereby some species persist for a time in a habitat patch following landscape-level degradation yet this degradation eventually drives their patch-level extinction

(Tilman et al., 1994). Extinction debt is an important consideration for conservation planning because without active intervention, even protected areas will continue to lose species (Kuussaari et al. 2009). The debt means current inventories of species may mask the full effects of habitat destruction. Yet while these species persist, there may still be time to employ actions such as habitat restoration that could prevent these extinctions.

While the extinction debt is a simple concept and is widely accepted (Halley et al. 2016, Thompson et al. 2019, Watts et al. 2020), testing for it in the field is not straightforward (Kuussaari et al. 2009, Figueiredo et al. 2019). Although empirical studies of the extinction debt have increased in recent years, research in this area is still limited and conclusions are varied (Figueiredo et al. 2019). For example, Adriaens et al. (2006) found no evidence of a plant extinction debt in Belgian grasslands, yet Saar et al. (2012) identified a debt within the same habitat type in Estonia. Similarly, evidence for the existence of an extinction debt in Swedish semi-natural grasslands is conflicting (Lindborg and Eriksson 2004, Oster et al. 2007). Disparities between such studies could be due to differences in the methodology employed, which is often limited by the availability of high quality historical data.

Kuussaari et al. (2009) identified five methods to detect an extinction debt. Three of these - Past Habitat, Past Communities and Stable Habitats (Box 4.1; my nomenclature) - use species-area relationships (SAR), which relate species numbers in habitat patches to habitat area. These SAR methods have the advantage of considering the whole community rather than single species approaches (e.g. Halley et al. 2016). These methods differ, however, in their assumptions and the amount of data used. Where more comprehensive data on past and current biodiversity patterns and landscape structure are available, a more reliable evaluation of the extinction debt will be possible (Kuussaari et al. 2009). Of the SAR approaches, the “Past Habitat” method is probably the least reliable, as no information on past species complements is used, nor can the magnitude of extinction debt be calculated. This method also assumes communities in past landscapes were at equilibrium. Despite this shortcoming, a review by Figueiredo et al. (2019) revealed that this was one of the most commonly employed methods to test for extinction debt; probably, because of the relatively modest data requirements. The “Stable Habitats” method can be considered more reliable as it uses much the same information as for the Past Habitat method but adds a contrast between putatively stable and unstable landscapes. However, stable landscapes are assumed to be at equilibrium and further assumptions are required for defining a stable landscape. The “Past Communities” method on the other hand might be considered the most reliable of the three, since the relationship between the past species richness and habitat area can be used to calculate the expected species richness in the current landscape. However, past biodiversity estimates are scarce, and thus very few studies have employed this method (Cowlishaw 1999, MacHunter et al. 2006). Of the 58 extinction debt studies published between 2009 and 2017 examined in Figueiredo et al. (2019), none used the Past Communities method.

If a study fails to detect an extinction debt, it is important to understand whether there is an issue with the method used or whether there really is no extinction debt. However, empirical studies that have used SAR methods rarely compare methods to determine whether they give similar conclusions (Figueiredo et al. 2019). Of the few studies that have done so, all compared the Past Habitat and Stable Habitats methods and all found that both approaches led to the same conclusions in the specific study systems (Piqueray et al. 2011a, Guardiola et al. 2013, Soga and Koike 2013). None of these studies, however, included the possibly more reliable Past Communities method. Kuussaari et al. (2009) highlighted the need for comparing the performance of these three methods in the same study systems, yet to date this remains unaddressed. Such an approach can reveal whether the detection or not of extinction debts using different methods across numerous study systems is robust, and to develop best practice towards future extinction debt evaluation.

Another potential explanation for differences in the conclusions from extinction debt studies is the selection of species for analysis. Habitat specialists are expected to be more sensitive to changes in that habitat (Watts et al. 2020) and thus the inclusion of generalist species that can use other habitats in the landscape could mask any extinction debt (Kuussaari et al. 2009). For instance, butterfly specialists showed an extinction debt in urban areas in Tokyo, whereas generalists did not (Soga and Koike 2013). In contrast, some studies have detected an extinction debt for both specialist and generalist species (Cousins and Vanhoenacker 2011, Bommarco et al. 2014).

Most extinction debt studies consider communities within a single habitat type across a landscape (Vellend et al. 2006, Lira et al. 2012, Guardiola et al. 2013, Rédei et al. 2014) and the habitat types studied are not representative of the range that exist. Most extinction debt research has been in Europe (Figueiredo et al. 2019) and, even here, there has been a disproportionate research effort on calcareous grasslands (Adriaens et al. 2006, Piqueray et al. 2011a, Saar et al. 2012, Huber et al. 2017). Most likely, this is because calcareous grasslands are one of the most species-rich temperate communities (Wilson et al. 2012), and are ideal for testing for extinction debt since they are often highly fragmented and contain many specialist species. Extinction debts in other habitats which have different patterns of degradation are relatively unknown. For example, heathland extinction debt studies have been limited to Belgium, where the detection of a debt has been equivocal (Piessens and Hermy 2006, Cristofoli et al. 2010a, Cristofoli et al. 2010b). This unrepresentative sample raises the question of whether the communities within habitats focused upon may bias conclusions about the prevalence of extinction debts. If extinction debt methods are to be evaluated, this needs to be examined across multiple habitats types in the same study.

In this study, I apply and compare three SAR methods (Box 4.1) for the detection of an extinction debt, using vascular plant communities in three habitat types in a rural landscape in the UK: calcareous grassland, heathland and broadleaved woodland. These three habitats have experienced different trajectories of change over the last 90 years, in a landscape that has undergone profound changes (Hooftman and Bullock 2012). The greatest losses in habitat area are evident for calcareous grassland, whilst heathland also underwent decline, albeit less severely (Ridding, Watson, et al. 2020, Chapter 2). Some small gains in woodland area occurred through planting, though this new habitat is likely not yet ecologically equivalent to what has been lost. Evaluating the SAR methods across habitats with different extents of degradation within the same study system, facilitates a reliable examination of the occurrence of extinction debts. I predict the following:

(i) The three SAR methods lead to the same inferences about extinction debts.

(ii) Strict habitat specialists are more likely to show extinction debts than more generalist species.

(iii) The habitat type that has undergone the most severe decline in area – calcareous grassland – is more likely to have a large and detectable extinction debt.

Box 4.1. SAR methods to evaluate extinction debts (adapted from Kuussaari et al. 2009)

“Past Habitat” method: Detection of extinction debt using past and present habitat characteristics

This relates the current species richness to habitat patch characteristics in past *vs* present landscapes, though the magnitude of the extinction debt cannot be estimated. An extinction debt is detected if the current species richness is better explained by the past landscapes compared with present landscape variables. For example, Cousins et al. (2007) examined past and present areas of semi-natural grassland patches in Sweden, but found no relationship between current species richness and habitat area from 100 years ago, suggesting no extinction debt was present.

“Stable Habitats” method: Estimating extinction debt by comparing present-day stable and unstable habitat patches

This requires the same data inputs as the Past Habitat method, but quantifies the magnitude of an extinction debt by using the equilibrium species number in habitat patches which have remained more constant in area to predict the expected species number for habitat patches that have undergone a decline in area. The magnitude of the extinction debt is the difference between predicted and observed species richness. For instance, Helm et al. (2006) used species-area relationships in stable calcareous grassland sites to predict species richness in sites that had declined considerably in their habitat area (unstable sites). They found the extinction debt estimated for individual grasslands was around 40% of their current species number.

“Past Communities” method: Estimating extinction debt based on past and present species richness and habitat characteristics

In addition to the data for the above methods, data on past species richness is required for this method. This allows for a more precise prediction of current species richness, which is based on the relationship between past habitat area and past species richness. The expected species richness is calculated using the past SAR relationship and the difference between this and the observed species richness gives the magnitude of the extinction debt. For example, Machunter et al. (2006) used bird species richness data and land use data from both the 1980s and 2000s in south-eastern Australia and found evidence of an extinction debt.

4.3. METHODS

The SAR methods require information on species richness in a number of habitat patches at the present day and also in the case of the Past Communities method, at some point in the past. Data are also needed on habitat area for the corresponding time periods in the past and present.

4.3.1. Study landscape

I conducted the study in Dorset, a predominantly rural county on the south coast of England (Figure 4.1), with a historical area (pre-1974) of ca. 2500 km^2 (Hooftman and Bullock, 2012). In the 1930s, prior to rapid intensification of land use, semi-natural habitats, including calcareous grassland, neutral grassland, heathland and broadleaved woodland, dominated the Dorset landscape. In the decades following the Second World War, considerable proportions of these semi-natural habitats were lost, predominately to arable and agriculturally-improved grasslands. The three habitat types differed greatly in their trajectories of change between 1930 and 2015. Calcareous grassland suffered the greatest losses (70% of sites lost), whereas over 50% of heathland sites were lost (Ridding, Watson, et al. 2020, Chapter 2). Conversely, due to tree planting, the number of broadleaved woodland sites increased by 3% during the same 85 year period.

4.3.2. Species data

In the 1930s Professor Ronald Good undertook a systematic survey of vascular plant species, using the ‘stand’ method, at 7575 sites that were evenly scattered across Dorset. Stands were considered to be ‘…reasonably distinct topographical and ecological entit[ies]…’ (Good 1937). A subset of these sites, ranging in size from 0.04 ha to 32.24 ha were re-surveyed between 2008 and 2010. Sites that remained classifiable as the original habitat type comprised 65 heathlands (Diaz et al. 2013), 88 calcareous grasslands (Newton et al. 2012), and 86 woodlands (Keith et al. 2009). The re-surveys were designed to match Good’s methodology as closely as possible. See Diaz et al. (2013), Keith et al. (2011, 2009) and Newton et al. (2012) for further details.

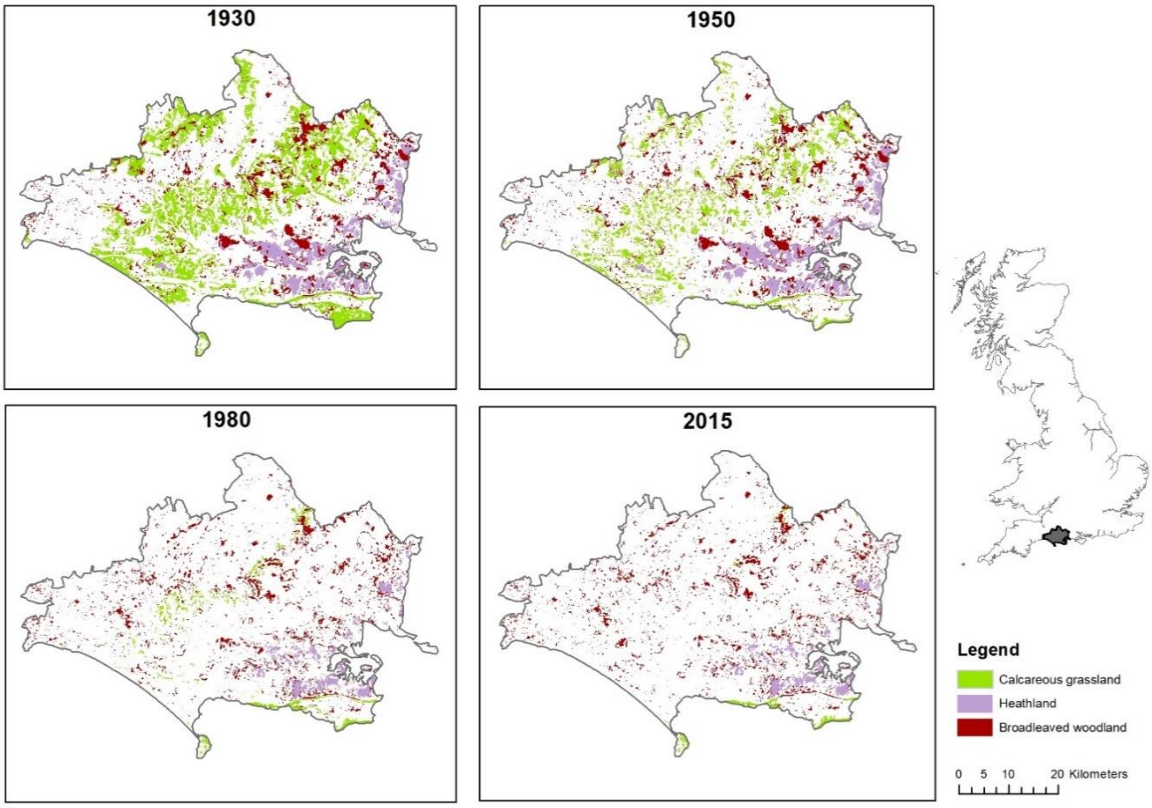

Figure 4.1 The extent of calcareous grassland, heathland and broadleaved woodland in Dorset, southern England in 1930 (Hooftman and Bullock 2012), 1950 (Ridding et al. 2020, Chapter 3), 1980 (Ridding et al. 2020, Chapter 3) and 2015 (Rowland et al. 2017).

4.3.3. Present and past landscape composition

I determined the extent of calcareous grassland, heathland and broadleaved woodland in the past and present using a time-series of landscape maps generated in Chapter 3 (Ridding, Newton, et al. 2020). I used the 1930s map produced by Hooftman and Bullock (2012) and the CEH Land Cover Map 2015 (LCM2015) (Rowland et al. 2017) to produce two intermediate maps for 1950 and 1980 at 100 m resolution, thereby generating a four-step time series for Dorset (Figure 4.1). To define each habitat patch for the SAR analyses, I calculated the area of calcareous grassland, heathland and broadleaved woodland for 1930, 1950, 1980 and 2015 within a 1 km buffer around each survey site (including the site itself, where site is the area in which plant species were recorded) using ESRI ArcGIS v10.4 (© ESRI, Redlands, CA). I chose the 1 km value as representing an area that would influence plant species richness at the survey site (Cousins et al. 2007; Ellis & Coppins 2007;

Hooftman et al. 2016). Some calcareous grasslands were not detected by the LCM2015, since small areas of semi-natural habitat are often undetected in this dataset, which has a minimum mappable unit of 0.5 ha (Ridding et al. 2015). To address this issue, I combined the LCM2015 with calcareous grassland maps from Natural England's Priority Habitats' Inventory (Natural England 2015). Further improvements were also made to the 1950 map (Appendix C.1). I omitted sites that did not coincide with the equivalent land cover in the landscape time-series. This procedure gave a total of 66 calcareous grassland, 62 heathland and 86 broadleaved woodland sites for further analysis.

4.3.4. Data analysis

I tested for extinction debt signals between 1930 and 2015 using the three methods. In addition, where the method enabled additional time periods to be included – 1950 and 1980 for Past Habitat and 1950 for Stable Habitats – I used these periods to assess if extinction debt was still detected, and therefore not just associated with a single arbitrary time period (see Appendix C.1). There was a slight time difference between the contemporary species richness within sites (2008-2010) and contemporary landscape (2015) datasets. However, it is very unlikely that there were any significant changes to habitat areas during 2008 and 2015, given that little change was detected in the areas of semi-natural habitats between 1990 and 2015 in Dorset (Ridding, Watson, et al. 2020, Chapter 2). I undertook these analyses for three species groups, classified using the habitat associations of Hill et al. (2004). Where a plant species was associated with the relevant habitat (calcareous grassland, heathland, broadleaved woodland) it was defined as a "habitat specialist", whereas if the species was associated with the relevant habitat and that habitat only it was a considered a "strict habitat specialist". Thus the latter group is more specialised. These two specialist groupings were exclusive. The final target group for the analysis included all plant species (i.e. the two specialist groups plus all other species), to mirror analyses that simply consider all species (Guardiola et al. 2013, Soga and Koike 2013).

Past Habitat: I applied the Past Habitat method using the log 10 of past and contemporary areas of each habitat patch (area within 1 km buffer – see Present and past landscape composition) and the log 10 of site area (area of the Good site in which plant species were surveyed – see Species data) as the independent variables to explain the contemporary species richness at each site. Site area was included to account for the differences among sites in the area that was surveyed for plant species (according to how Good defined the stand in the 1930s). Site area was not strongly correlated with habitat patch area for any of the habitat types ($r < 0.60$). I generated generalized linear models (GLMs) with a Poisson distribution and log link (Zuur et al. 2009) in R (R Core Team 2019). As in many other extinction debt analyses, the independent variables i.e. the area of habitat in 1930, 1950, 1980 and 2015 were all strongly correlated ($r > 0.60$), so I analysed each variable in a separate model. I selected the best of those models, and thus the time period which best predicted contemporary species richness, as that with the lowest second-order Akaike Information Criterion for small sample sizes (AICc), with a difference greater than 2 indicating a better fit (Burnham and Anderson 2002). AICc was calculated using the "AICcmodavg" package (Mazerolle 2020), whilst McFadden's Pseudo-R^2 was computed using the "pscl" package (Jackman 2015).

Stable Habitats: I compared the contemporary plant species richness of "stable" (less than 40% loss in area since the historical date) and "unstable" habitat patches (more than 40% loss in area since the historical date (1930 or 1950). Other authors have classified stable *vs* unstable patches using thresholds of from 10-40% (Fahrig 2003, Helm et al. 2006, Guardiola et al. 2013). For Dorset, a 40% threshold ensured a more even and consistent sample size for stable and unstable patches across the three habitats. Where the sample size allowed, further analysis using a threshold of 20% was also undertaken (see Appendix C.2). For each habitat type I generated two separate GLMs with a Poisson distribution using the log of patch and site areas as independent variables to estimate species richness in stable patches in 2015. The first GLM used the past patch area, whilst the second model used the contemporary patch area. Next, I used the resulting parameter estimates from the two models for stable patches to predict species richness in 2015 in the unstable patches, using their contemporary area as the predictor variable. The extinction debt is the excess of observed species in comparison with the predicted number of species. The two models (one using the past patch area, and one using the current patch area) bracket the magnitude of the extinction debt, where the model based on past landscape structure probably gives an overestimate of extinction debt, whilst the model based on the contemporary landscape probably gives an underestimate (Helm et al. 2006). The significance of the extinction debt (i.e. observed number of species – predicted number of species) was determined using a Wilcoxon signed-rank test, since parametric assumptions were not met, as also seen in Soga and Koike (2013).

Past Communities: I generated GLMs with a Poisson distribution to determine the relationship between the log of past habitat area and the past species richness for each habitat type, using species richness from each site in the 1930s and the corresponding habitat patch (area within 1km buffer) as individual sampling points. Again, the log of site area was also included to account for differences in the area surveyed for plants. This relationship was then used to predict current species richness, using the contemporary area as the explanatory variable. As for the Stable Habitats method, the extinction debt is the excess of observed species in comparison with the predicted number of species, with the significance determined by a Wilcoxon signed-rank test.

4.4. RESULTS

A total of 309 species were identified in calcareous grasslands (82 habitat specialists and 43 single-habitat specialists), 352 in the heathlands (29, 7) and 443 (132, 54) in the broadleaved woodlands across the 1930 and 2008-10 surveys. The respective habitat area within the 1 km buffer around the study site had declined by a mean of 73% in calcareous grassland and 46% in heathland, but increased by a mean of 2% in woodland.

Detection of extinction debts varied between the methods employed and within the different habitat types (Table 4.1). A significance threshold of $P \leq 0.05$ was employed but exact P values and effect sizes from each of the GLMs for the three methods are given in Tables 4.2-4.4. Using the Past Habitat method, past habitat area explained contemporary species richness better than the current habitat area for calcareous grassland, as indicated by the lower AICc for 1930 compared with 2015, across both specialist groups and all species, suggesting extinction debts exist (Table 2). This was still evident when habitat areas in 1950 and 1980 were used, but the effects were weaker (Appendix C.1). The Past Habitat method suggested a heathland extinction debt only for all species, whereas for woodland current habitat area explained contemporary species richness better for all species, implying no extinction debt present. There was little difference between the 1930 and 2015 models for woodland and heathland specialists groups.

For the Stable Habitats method I divided habitat patches into stable and unstable patches of calcareous grassland (12 stable and 54 unstable), heathland (43 stable and 19 unstable) and woodland (79 stable and 7 unstable). The mean area retained between 1930 and 2015 in stable and unstable sites was respectively 69% and 17% for calcareous grassland, 67% and 25% for heathland and 108% and 27% for woodland. Extinction debts were identified for calcareous grassland using the Stable Habitats method, whereby the observed plant species richness values were significantly higher than predicted (Figure 4.2, Table 4.3) for all three species groups. An extinction debt was also suggested using the past model within the Stable Habitats method for all species in heathland, though this was not consistent with the current model, where contemporary habitat area was used a predictor variable rather than past habitat area. The opposite pattern, whereby the current model revealed an extinction debt but not the past, was found when using habitat area in 1950 for all heathland species (Appendix C.1). There were no other significant differences between observed and predicted species richness for the other heathland species groups or woodland (Table 4.1).

By contrast to the other methods, the Past Communities method showed similar results across all three habitat types for the specialist species groups (Figure 4.2, Table 4.1), whereby extinction debts were detected for both habitat and strict habitat specialists in calcareous grassland and woodland, albeit only for strict habitat specialists in heathland. The mean total species extinction debt was similar for strict habitat specialists in calcareous grassland (3.13 species) and woodland (3.28 species) but much lower in heathland (0.35 species) (Figure 4.2). An extinction debt was also evident across all species in calcareous grassland using this method, however habitat patch area explained very little of the variance in the regression model (Table 4.4), which was used to predict species richness in the present. For heathland and woodland however, the predicted species richness for the all species group was greater than the observed richness, which suggests no extinction debt (Table 4.4).

Table 4.1 Summary table to show which methods (Box 4.1) showed an extinction debt ("Yes") or no evidence of an extinction debt ("No") for the three species group classifications (strict habitat specialist, habitat specialist, and all species) in the three habitat types (calcareous grassland, heathland and woodland) between 1930 and 2015. For the "Past Habitat" method if the AICc was lower for 1930 compared with 2015, an extinction debt was concluded. Extinction debt for the "Stable Habitats" and "Past Communities" methods, was indicated by a significantly greater observed species richness compared with the predicted species richness.

		Past Habitat	Stable Habitats	Past Communities
Calcareous	Strict habitat specialist	Yes	Yes	Yes
	Habitat specialist	Yes	Yes	Yes
	All species	Yes	Yes	Yes
Heathland	Strict habitat specialist	No	No	Yes
	Habitat specialist	No	No	No
	All species	Yes	No	No
Woodland	Strict habitat specialist	No	No	Yes
	Habitat specialist	No	No	Yes
	All species	No	No	No

Table 4.2 Extinction debt evaluated using the "Past Habitat" method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. The coefficient and standard error have been exponentiated for each regression model and are presented along with the p-value for the patch variable, AICc and R^2 value.

	Species groups	Year	Coefficient	SE	P	AICc	R^2
Calcareous grassland	Strict habitat specialist	1930	1.29	1.07	<0.001	544.22	0.044
	Strict habitat specialist	2015	1.05	1.04	0.183	556.90	0.022
	Habitat specialist	1930	1.25	1.05	<0.001	661.87	0.047
	Habitat specialist	2015	1.01	1.03	0.662	682.62	0.017
	All species	1930	1.08	1.03	0.029	709.16	0.025
	All species	2015	0.98	1.02	0.312	713.00	0.019
Heathland	Strict habitat specialist	1930	1.34	1.26	0.204	183.31	0.120
	Strict habitat specialist	2015	1.28	1.15	0.080	181.77	0.127
	Habitat specialist	1930	1.29	1.16	0.081	259.29	0.153
	Habitat specialist	2015	1.23	1.09	0.025	257.13	0.160
	All species	1930	1.30	1.07	<0.001	561.23	0.036
	All species	2015	1.00	1.03	0.927	579.24	0.005
Broadleaved woodland	Strict habitat specialist	1930	0.98	1.04	0.628	485.95	0.017
	Strict habitat specialist	2015	0.96	1.04	0.361	485.36	0.019
	Habitat specialist	1930	0.96	1.02	0.054	626.85	0.021
	Habitat specialist	2015	0.94	1.03	0.018	625.90	0.024
	All species	1930	0.94	1.01	0.001	780.09	0.102
	All species	2015	0.92	1.02	<0.001	775.28	0.107

Table 4.3 Extinction debt evaluated using the "Stable Habitats" method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. Model indicates whether past or current patch area was used to predict contemporary species richness. The exponentiated coefficient and standard error, and R^2 values are presented for each regression model. Extinction debt is calculated as the difference between the numbers of predicted and observed plant species, alongside the range and the p-value resulting from a Wilcoxon test comparing the two. Those in bold reveal where an extinction debt is suggested.

	Species groups	Model	Coefficient	SE	R^2	Extinction debt		
Calcareous grassland	Strict habitat specialist	Current	**2.62**	**1.47**	**0.123**	**8.02**	**(-4.28 ~ 25.15)**	**<0.001**
	Strict habitat specialist	Past	**1.18**	**1.20**	**0.074**	**5.60**	**(-7.42 ~ 21.01)**	**<0.001**
	Habitat specialist	Current	**2.48**	**1.32**	**0.153**	**14.25**	**(-8.00 ~ 42.15)**	**<0.001**
	Habitat specialist	Past	**1.28**	**1.15**	**0.100**	**11.44**	**(-8.89 ~ 36.50)**	**<0.001**
	All species	Current	**1.04**	**1.20**	**0.158**	**11.92**	**(-24.20 ~ 45.73)**	**<0.001**
	All species	Past	**1.00**	**1.09**	**0.158**	**10.48**	**(-25.45 ~ 43.52)**	**<0.001**
Heathland	Strict habitat specialist	Current	1.21	1.26	0.072	0.05	(-0.75 ~ 0.81)	0.623
	Strict habitat specialist	Past	1.24	1.34	0.072	0.22	(-0.61 ~ 0.99)	0.090
	Habitat specialists	Current	1.20	1.16	0.124	-0.07	(-3.12 ~ 2.16)	0.900
	Habitat specialists	Past	1.26	1.21	0.124	0.39	(-2.52 ~ 2.67)	0.241
	All species	Current	1.24	1.07	0.038	5.81	(-10.22 ~ 37.84)	0.123
	All species	**Past**	**1.42**	**1.10**	**0.058**	**9.58**	**(-6.44 ~ 42.11)**	**0.011**
Broadleaved woodland	Strict habitat specialist	Current	0.99	1.04	0.020	2.56	(-3.91 ~ 7.46)	0.219
	Strict habitat specialist	Past	0.98	1.04	0.021	2.48	(-3.92 ~ 7.38)	0.219
	Habitat specialists	Current	0.96	1.03	0.024	4.11	(-7.61 ~ 15.19)	0.438
	Habitat specialists	Past	0.95	1.02	0.026	3.96	(-7.80 ~ 15.12)	0.438
	All species	Current	0.94	1.02	0.115	3.66	(-9.64 ~ 21.09)	0.438
	All species	Past	0.94	1.02	0.117	3.62	(-10.15 ~ 21.25)	0.438

Table 4.4 Extinction debt evaluated using the "Past Communities" method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. The exponentiated coefficient and standard error, and R^2 values are presented for each regression model. Extinction debt is calculated as the difference between the numbers of predicted and observed plant species, alongside the range and the p-value resulting from a Wilcoxon test comparing the two. Those in bold reveal where an extinction debt is suggested.

	Species groups	Coefficient	SE	R^2	Extinction debt		
Calcareous grassland	Strict habitat specialist	**1.15**	**1.07**	**0.026**	**3.13**	**(-10.00 ~ 19.26)**	**<0.001**
	Habitat specialist	**1.11**	**1.05**	**0.023**	**5.86**	**(-15.63 ~ 30.85)**	**<0.001**
	All species	**1.00**	**1.04**	**0.001**	**14.89**	**(-23.01 ~ 46.70)**	**<0.001**
Heathland	Strict habitat specialist	**0.91**	**1.26**	**0.103**	**0.35**	**(-1.74 ~ 2.89)**	**0.009**
	Habitat specialists	0.96	1.15	0.095	0.32	(-3.84 ~ 4.74)	0.242
	All species	0.84	1.05	0.089	-3.58	(-61.36 ~ 23.44)	0.070
Broadleaved woodland	Strict habitat specialist	**0.92**	**1.04**	**0.031**	**3.28**	**(-6.75 ~ 11.93)**	**<0.001**
	Habitat specialists	**0.92**	**1.03**	**0.048**	**4.25**	**(-17.45 ~ 19.16)**	**<0.001**
	All species	0.91	1.02	0.127	-5.13	(-40.85 ~ 28.96)	0.002

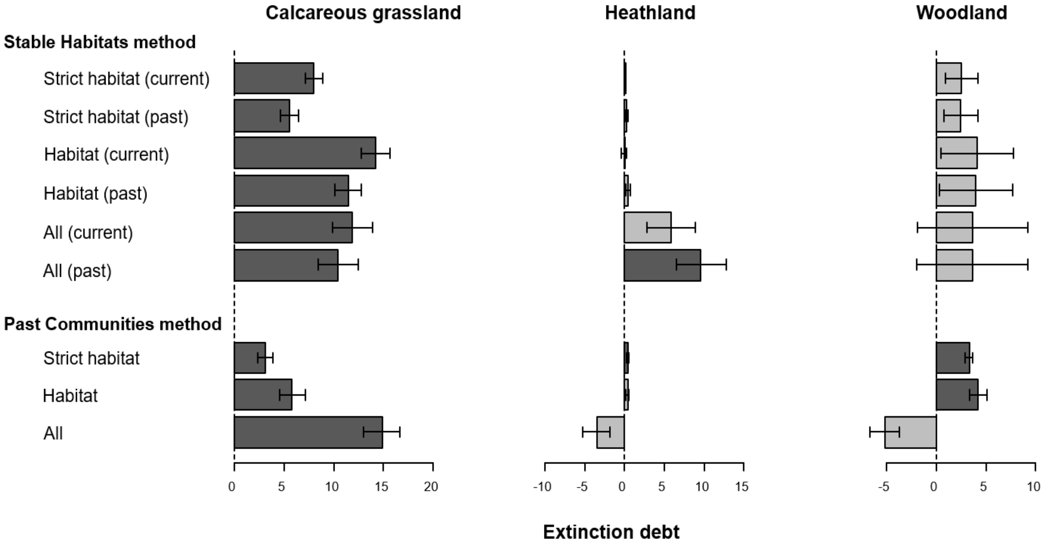

Figure 4.2 Extinction debt (± SE), in terms of the mean number of species across sites, as assessed using two methods between 1930 and 2015 across three habitat types; calcareous grassland, heathland and woodland (see also Table 4.3 and 4.4). For the "Stable Habitats" method, "(current)" and "(past)" indicate which patch area was used to predict contemporary species richness. Bars in dark grey indicate models where the observed species richness is significantly greater than the predicted species (*P* < 0.05), i.e. there is an extinction debt.

In summary, calcareous grassland was the only habitat in which an extinction debt was detected between 1930 and 2015 using all three methods (Table 4.1). The greatest mean extinction debt of 14.89 species was detected for all species using the Past Communities method for this habitat between 1930 and 2015 (Figure 4.2). An extinction debt was detected for heathland using two of the methods, whereas only the Past Communities detected an extinction debt for woodland.

4.5. DISCUSSION

4.5.1. Differences between three extinction debt methods

I found evidence for extinction debts in plant communities across three temperate habitats; calcareous grassland, heathland and woodland. However, my analysis showed that detecting an extinction debt is greatly dependent on the method employed, contrary to my first prediction; that the three SAR methods lead to the same inferences about extinction debts. The Past Communities method was the only one to suggest an extinction debt across all three habitat types. This method is used rarely owing to the extra data requirements, specifically past species richness data, but has demonstrated extinction debts in other study systems (Cowlishaw 1999, MacHunter et al. 2006). The other two methods produced different results, with the Past Habitat method suggesting extinction debts in calcareous grassland and heathland (for all species only), whilst the Stable Habitats method detected a debt only in calcareous grassland. While inconsistencies among methods have not been found in previous studies, these studies are few and they compared only the Past Habitat and Stable Habitats methods (Guardiola et al. 2013, Soga and Koike 2013), which are largely similar approaches. For example, in Belgian calcareous grasslands, Piqueray et al. (2011a) found extinction debts with both methods.

The Past Communities approach is likely the most powerful because data about the relationship between past species richness and past habitat area is utilised (Kuussaari et al. 2009). A SAR is constructed using historical data and this is contrasted with species data in the contemporary landscape. By contrast, the other two methods simply ask whether past landscape characteristics – habitat areas in this case – are a better predictor of contemporary species count data than contemporary landscape characteristics. Because landscape characteristics are correlated over time, as this research and other studies (Husáková and Münzbergová 2014, Rédei et al. 2014) show, these methods rely on an assumption that species richness was tightly linked to landscape characteristics at the chosen point in the past and this signal remains strong in the contemporary species record. The Past Communities method does not rely on finding some relationship between present species data and past landscapes, and this may explain why this suggested extinction debts where the other methods did not. Indeed, the fact that the Past Communities method identified extinction debts in all habitat types suggests that the use of the Past Habitats and Stable Habitats methods could increase uncertainty in the detection of extinction debts. This has important implications for conclusions about the existence and prevalence of extinction debts more broadly. This problem is further exacerbated by the fact that the Past Habitats and Stable Habitats methods are more commonly employed in the literature (Figueiredo et al. 2019), probably owing to their less demanding data requirements. The threshold used in the Stable Habitats method is also an important cause of uncertainty, since the magnitude of extinction debt can be very sensitive to the threshold selected (Piqueray et al. 2011b). However, the additional analysis using a threshold of 20% for calcareous grassland (Appendix C.2), also indicated an extinction debt across the three species groups, as found when employing a 40% threshold. Another factor which may influence the detection of an extinction debt is the time period selected in the past, which is usually governed by availability of historical data rather than hypotheses about the rate at which species are lost (Bagaria et al. 2015, Neumann et al. 2017). Efforts over recent years have increased the number of historical biodiversity datasets (e.g. Vellend et al. 2013; Dornelas et al. 2014). While these vary in quality and so must be used with care (Cardinale et al. 2018), they provide the potential for a more systematic and robust analysis of extinction debts using the Past Communities method. Data on landscape composition for the corresponding time period is also required, which can be challenging to attain. However, recently a number of studies have utilised historical national maps to explore changes in land cover (Kaim et al. 2016, Chen et al. 2019), which could be extended to extinction debt analysis providing suitable species data are available.

4.5.2. Extinction debt detection using different species groups

Using the Past Communities method, I detected extinction debts for the two types of specialist species in calcareous grassland and woodland, and for the strict habitat specialist in heathland, supporting my second prediction, indicating strict habitat specialists are more likely to show extinction debts than more generalist species. This result supports the suggestion that only specialist species should be included in extinction debt analyses (Kuussaari et al. 2009). While the SAR approach is valid for specialists and generalists because both will react to loss of their habitat, the inclusion of generalist species which can persist in other habitats than that focussed on is likely to obscure relationships between species number and area of the focal habitat. If generalists are persisting well in the landscape by living in other habitats, then this may lead to a conclusion of no extinction debt. Generalists may exhibit an extinction debt where the focal habitat is very different to other habitats in the landscape, meaning the generalists persist poorly elsewhere in the landscape. This may explain the extinction debt detected for generalists in calcareous grassland by all three methods. This is consistent with other studies, where the Past Habitat and

Stable Habitats methods detected extinction debts for all species and for specialists in semi-natural grasslands (Cousins and Vanhoenacker 2011, Piqueray et al. 2011a).

4.5.3. Extinction debt within three habitat types

Calcareous grassland was the only habitat for which an extinction debt was suggested by all three methods and for all species groups. Furthermore, the debt in calcareous grassland was greater than those in woodland and heathland, estimated using the Stable Habitats and Past Communities methods. These findings support my third prediction; calcareous grassland exhibits the greatest extinction debt. Numerous other studies have also identified the presence of an extinction debt within this habitat type across Europe (Helm et al. 2006, Krauss et al. 2010, Piqueray et al. 2011a). By comparison with the other habitats, my study suggests that the extent of the extinction debt in calcareous grassland is due to the combination of a history of severe degradation with the richness of specialist species. Heathland, on the other hand, has experienced considerable, although lesser, degradation in the region but I did not find extinction debt for this habitat across all methods. Heathland specialists are generally long-lived and have a persistent seedbank (Piessens and Hermy 2006, Saar et al. 2012) like specialists in calcareous grassland, however the number of such specialist species is much lower than in calcareous grassland (43 for calcareous grassland specialists only *vs* 7 in heathland), which may explain the weaker signal of an extinction debt for heathland. Furthermore, the differences between calcareous grassland and heathland may be linked to the colonization and connectivity of populations and metapopulations (Figueiredo et al. 2019), because heathlands are more tightly clustered in Dorset than are calcareous grasslands (Hooftman & Bullock 2012). The surrounding landscape may also be important. The SAR methods employed in this study assume that the species cannot survive outside their habitat, and this is probably true of the strict habitat specialists. Other SAR methods e.g. cSAR (Pereira et al. 2014) recognise that species may not be constrained to fragments of their habitat, which could be an important consideration in future extinction debt studies.

I detected an extinction debt in woodlands similar in magnitude to that in calcareous grassland, albeit only using the Past Communities method. Woodland did not suffer the severe declines in habitat area over the whole of Dorset, as seen for calcareous grassland and heathland, but instead increased over time, due to planting of new woodland, which countered losses of old woodland. The planting of new woodland seems to have been rather scattered across Dorset, and not focussed on increasing woodland around existing patches (Hooftman and Bullock 2012). As a result, of the 86 woodland patches, 52 suffered declines in woodland area from past to present. The finding of an extinction debt for woodlands reflects the local losses and highlights the fact that to avoid the paying of the extinction debt, restoration needs to enhance the landscape around existing habitat (Newmark et al. 2017).

4.6. CONCLUSIONS

This study is the first to compare three SAR methods for detecting an extinction debt and also across multiple habitats. Considering the results from the most data intensive, and hence presumably most reliable method (Past Communities), all habitat types demonstrated an extinction debt. The detection and magnitude of this debt however, differed among habitats, species with different levels of habitat specialisation, and method used. This result has important implications for confidence in reported extinction debts and emphasises the need for accurate extinction debt information using the best quality data. In my study, extinction debts were most clear for the habitat which had suffered the most severe decline (calcareous grassland) using all methods. However, two of these methods (Past Habitat, Stable Habitats) did not consistently reveal a debt where the habitat loss was less severe (heathland) or where the habitat had actually increased over time (woodland). This outcome suggests that unless habitat loss is severe, the two methods that do not incorporate any past species information have a limited capacity for detecting extinction debt. This has important implications for conservation in the future, where restoration opportunities may be missed if an extinction debt is thought not to be present.

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CHAPTER 5

Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016

5.1. ABSTRACT

Analysis of long-term vegetation change is limited. Furthermore most studies evaluating change only examine two snapshots in time, which makes it difficult to define rates of change and accurately assess potential drivers. To assess long-term change in calcareous grassland over multiple time periods, I re-surveyed a transect study undertaken at Parsonage Down National Nature Reserve, Wiltshire, southern England in 1970 and 1990 by T. Wells. I examined differences in soil properties and species traits in each of the survey years to understand potential drivers of vegetation change, including nitrogen deposition and grazing management. There was a clear shift in species composition, combined with significant declines in species richness and diversity between 1970 and 2016, with the greater rate of change occurring between 1990 and 2016. A significant increase in soil total nitrogen was found, which was significantly associated with the decline in species diversity between 1970 and 1990. Significant changes in community-weighted mean traits were identified for plant height (increasing), specific leaf area (decreasing), grazing tolerance (decreasing) and Ellenberg N (decreasing) between 1970 and 2016. By using survey data from multiple time periods, the analysis suggests that N deposition may have contributed towards community changes between 1970 and 1990, as indicated by the change in soil properties and the associated decline in species diversity. Vegetation change between 1990 and 2016 is likely to be largely attributable to a decline in grazing pressure, indicated by the increase in taller species and a decrease in grazing tolerance.

5.2. INTRODUCTION

Habitat degradation is one of the main drivers of biodiversity loss worldwide (Newbold et al. 2015). Unlike habitat destruction, degradation involves a gradual decline in habitat quality, and can be difficult to detect. Furthermore, most studies examining habitat degradation or change over time only use a single or two snapshots in time (e.g. Diaz et al., 2013; Keith et al., 2009). This static approach makes it difficult to understand trajectories of change (Renard et al. 2015) or to assess potential drivers accurately. Understanding these drivers is essential for predicting future changes and consequently adapting management to mitigate these impacts in order to conserve habitats and their species.

Calcareous grassland is a classic example of a habitat that has undergone considerable destruction and degradation across Europe. The loss was particularly severe during the twentieth century (Fuller 1987, van Dijk 1991, Polus et al. 2007, Ridding et al. 2015) due to agricultural intensification or abandonment (Poschlod and Wallis de Vries 2002). For example, Fuller (1987) estimated that 97% of semi-natural grassland had been lost between 1932 and 1984 in England and Wales. Calcareous grasslands have high conservation value, supporting a high diversity of plant and animal species and providing multiple ecosystem services (Bullock et al. 2011).

The condition of remaining calcareous grasslands has also declined over time (Bennie et al. 2006, Diekmann et al. 2014, Stevens et al. 2016), with very few studies finding increases in species richness over time (Mitchell et al. 2017). Contemporary surveys, which assess the condition of vegetation at a single point in time, show that only 29% of lowland calcareous grasslands designated as Sites of Special Scientific Interest (SSSI) (or “Areas of Special Scientific Interest” in Northern Ireland (ASSI)) were in “favourable condition” in the UK (Williams 2006). A/SSSIs are the basic unit of statutory protection in the UK for areas of land selected for ‘special interest by reason of any of its flora, fauna, or geological or physiographical features’, with their condition assessed against a standardised ideal (JNCC 2015). These studies are useful for assessing current status, however they provide limited insight into detailed community changes, the rate of change over time and potential drivers of this.

Ecologists use three main approaches to examine drivers of vegetation change: controlled experiments, long-term monitoring or temporal re-surveys, and space-for-time substitutions (Elmendorf et al. 2015). For example, Maskell et al. (2010) used “space-for-time” substitution to understand temporal changes in grassland status using spatial differences in nitrogen (N) deposition. However, this method is often criticised and has been found to be less effective compared with time-based “before-after-control-impact” approaches (França et al. 2016). Other studies using long-term vegetation data from two snapshots in time have shown significant decreases in species richness (Bennie et al. 2006, Stevens et al. 2016) and shifts in species composition (Newton et al. 2012, Diekmann et al. 2014) in calcareous grasslands. These impacts have been attributed to possible management changes, climate and/or N deposition. Although perennial vascular plant assemblages are generally more stable than annual ones, caution should be taken when evaluating two time points, since this may reflect normal inter-annual variation or abnormal variation caused by unusual weather, for example. Useful indicators of drivers such as management, climate and N deposition can be derived from the traits of species present in the community (Smart et al. 2006, Keith et al. 2009). For example, specific leaf area (SLA) and plant height are relevant traits for understanding the effects of grazing pressure and N deposition, since more competitive plants typical of nutrient rich conditions are more likely to have a higher SLA and canopy height (Stevens, Smart, et al. 2011, Stevens et al. 2016). Weighted Ellenberg values of a vegetation community (Hill et al. 2004), particularly soil fertility (N), and soil acidity (R), have been shown to be sensitive to N deposition in other studies (Emmett et al. 2011, Rowe et al. 2017), although some find no relationship with Ellenberg N (Stevens et al. 2010). Despite this, Ellenberg N and R are often used to suggest the influence of N deposition on vegetation change (Newton et al. 2012, Diekmann et al. 2014).

However, using traits to attribute environmental change to particular drivers can be problematic, as they can vary in their sensitivity across spatial scales and may respond to multiple drivers (Ames et al. 2016, Shipley et al. 2016), thus contemporaneous direct measures of drivers are often preferable. Despite the number of long-term vegetation studies, few have examined detailed vegetation data across multiple time periods for calcareous grassland with measures of drivers at each interval. This would provide more reliable insights into factors influencing change over time, especially as this is likely to be driven by policy, biophysical, and socioeconomic characteristics, all of which will vary (Renard et al. 2015). Furthermore, if the levels of different drivers have changed over time, as has been reported for N deposition (Du 2016, Tipping et al. 2017), having multiple surveys may allow these shifting effects to be disentangled.

N deposition has been well documented as a driver of change in acidic grasslands using space-for-time approaches (Duprè et al. 2010, Maskell et al. 2010, Diekmann et al. 2014). However fewer clear findings have been reported for calcareous grasslands. For Britain, a space-for-time study examining the effects of atmospheric N deposition in heathland, acid, calcareous and mesotrophic grassland, found a significant reduction in species richness in acid grassland, however this was not identified for calcareous grassland (Maskell et al. 2010). A similar study by Diekmann et al. (2014) also reported no effect on species richness, but they did identify a shift in species composition in calcareous grassland in North-west Germany. N deposition is known to affect the status of grassland soils, where increases in soil N, decreases in the total C/N ratio and declines in base cations have been reported (Stevens, Manning, et al. 2011, Phoenix et al. 2012, Rowe et al. 2017). Because of this, soil properties are often used as indicators of N deposition.

Changes to the management of grasslands in recent decades, particularly grazing, are also suggested as one of the drivers of degradation in calcareous grassland (Williams 2006). Under-grazing can lead to scrub encroachment and the loss of indicator grassland species, whilst over-grazing can cause unpalatable species to dominate (Bullock et al. 2011). Other potential management influences include indirect nutrient enrichment through grazing improved and unimproved pastures together, or supplementary feeding, which can lead to a loss of plant diversity (Kirkham 2006).

Utilising records of past vegetation therefore provides an opportunity to quantify and understand the mechanisms behind long-term environmental change. In this study I repeat a detailed transect survey, originally recorded in the 1970s, to examine vegetation change over time and identify potential drivers. The original survey was led by Terry Wells in 1970 to investigate the floristic composition of calcareous grassland overlying a Celtic field system at Parsonage Down National Nature Reserve (NNR) in southern England. Celtic field systems are prehistoric agricultural systems, and where boundaries are still evident, as at Parsonage Down, this suggests that a field has never been ploughed (Rhodes 1950). In 1990, Wells and colleagues repeated the survey to examine if N deposition and its effects were apparent, although none were identified (Wells 1993). This study thus offers a rare assessment of long-term vegetation changes in calcareous grassland across three time points with complete supporting data for the close examination of drivers. Based on the evidence reviewed above I hypothesise that:

(i) Vegetation change between 1970 and 2016 is non-linear, reflecting changes in drivers over time.

(ii) Changes in soil properties over time are a consequence of N deposition and will be evident through increases in soil N and declines in base cations.

(iii) Changes in vegetation will reflect the soil status over time.

(iv) Changes in N deposition and grazing are evident through changes in the trait profile of the vegetation.

5.3. METHODS

5.3.1 Study Area

The survey was undertaken at Parsonage Down NNR, Wiltshire (51^o10’17”N, 1^o55’25”W). Parsonage Down was designated as an NNR and SSSI in 1973 and 1986 respectively, and consists of 188 ha of chalk grassland. Until 1979 the owner had farmed the land using traditional methods for 53 years, grazing it with both cattle and sheep, with stocking levels carefully controlled (Table 5.1). Under the subsequent ownership of Natural England, the statutory nature conservation body for England, the grassland has continued to be grazed with sheep and cattle, with no mineral fertiliser usage, however, the timings and numbers of cattle and sheep grazing have been more variable compared with earlier time periods (Table 5.1, Appendix Table D.1).

Table 5.1 The upper and lower estimates of the total number of cattle and sheep grazing at Parsonage Down between 1970 and 2016 using qualitative data from reserve managers (see Appendix Table D.1).

Time period	Cattle	Sheep
1970-1990	330-350	430
1990-2016	75-90	250-380

Modelled N deposition data shows a steady increase in total N deposited at Parsonage Down between 1800 and 1990, with a decline since the 1990s (Tipping et al. 2017) (Figure 5.1). The decline in N deposition across the UK since the 1990s is largely attributed to the reduction in industrial and vehicle emissions of nitrogen compounds, after new policy measures were introduced (RoTAP 2012), though reduced N has declined much less than oxidised N.

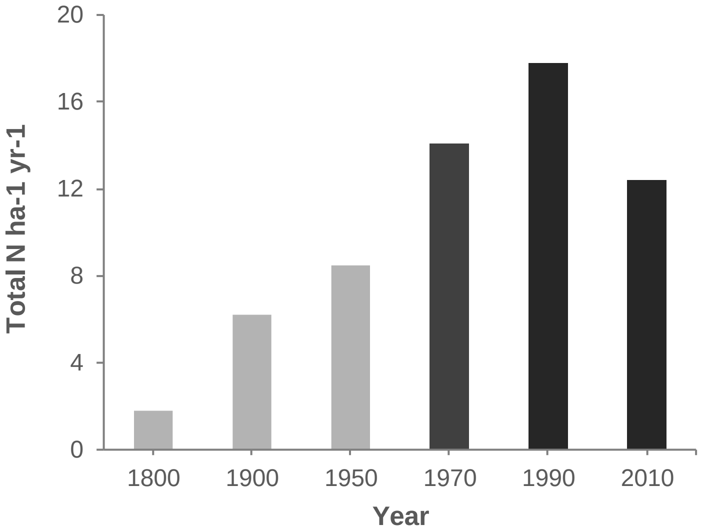

Figure 5.1 Total nitrogen deposition for the 5 km by 5 km grid square which includes Parsonage Down National Nature Reserve for six snapshot years between 1800 and 2010 (method described in Tipping et al. 2017). The years which correspond exactly (1970 and 1990) or closely (2016) to the survey periods are shown in black.

5.3.2. Survey Method

Four transects were set up in 1970; transects three and four measured 18.3 m, whilst transects one and two were 33.8 m and 31.1 m in length, respectively, to encompass the Celtic field boundaries. Vascular plant species were recorded using the Domin scale of Dahl and Hadač (1941), a system based on 10-cover/abundance categories devised for recording cover of species in a community, in 20 cm x 20 cm quadrats every 0.9 m on each of the four transects, giving a total of 115 quadrats. Vascular plants were identified to species level, with the exception of *Taraxacum* microspecies. The sward height was determined using the direct measurement method (Stewart et al. 2001). Twenty two soil samples were taken at 11 positions along each of the four transects (Appendix Table D.2), at two depths, 0-5 cm and 5-10 cm, using a corer of 3.5 cm diameter. The following soil properties were determined for each sample; pH, loss on ignition (LOI), exchangeable potassium (K), magnesium (Mg) and calcium (Ca), phosphate (PO_4-P) and total nitrogen (N). For further details on chemical analysis see Appendix Table D.3. Wells and colleagues re-surveyed the same quadrats in August 1990 and collected soil samples which were analysed in 1990 using the same methodology and locations as used in 1970 (Wells 1993).

In 2016 transects were accurately relocated by geo-referencing Wells' original survey maps with a 1:125 scale map (held at the Centre for Ecology & Hydrology (CEH), Wallingford, UK) showing the Celtic field systems, using archaeological GIS layers provided by the Defence Infrastructure Organisation, which also highlighted the same Celtic field boundaries. Reliably re-locating transects is essential when evaluating change over time, since imprecise locations can increase the likelihood of pseudo-turnover, where species may be incorrectly recorded as extinct or colonising due to misplacement (Fischer and Stöcklin 1997). The geo-referencing procedure was completed using ESRI ArcGIS v10.4 (© ESRI, Redlands, CA). Vegetation data and soil samples were collected in the same locations as the original survey during a similar time of year (June and August for the vegetation and soil sampling, respectively) and were analysed using the methodology outlined above. Grid references were recorded for the start and end of the four transects, accurate to ± 2 m (Appendix Table D.4).

5.3.3. Potential drivers of change

Measurements of soil properties (pH, LOI, exchangeable K, Mg and Ca, PO_4-P and total N), were evaluated for each survey year. These are important metrics for N deposition and may be considered a more direct method or a midpoint indicator ("links in the cause-effect chain") for evaluating the influence of N deposition, where a midpoint indicator indicates progress towards changes in biodiversity (the endpoint) (Rowe et al. 2017). I used community-weighted mean Ellenberg indicator values (Hill et al. 2004) for soil N, and soil R to examine the potential influence of N deposition on vegetation change (Emmett et al. 2011, Newton et al. 2012, Rowe et al. 2017). I also used database-derived values for a species' height (Hill et al. 2004), SLA (Kleyer et al. 2008) and grazing tolerance (Briemle et al. 2002) to assess the potential impact of grazing pressure (Grant et al. 1985, Bullock et al. 2001).

5.3.4. Data analysis

Vegetation data from the first two surveys (Wells 1993) were digitised from record cards archived at CEH. Nomenclature from the earlier surveys was adjusted to follow Stace (2010). To assess changes in individual species, I used two separate Chi-squared tests to test for changes in frequency between (1) 1970 and 1990, and (2) 1990 and 2016. Due to the large number of comparisons, P values were adjusted in order to control the false discovery rate using the method of Benjamini and Hochberg (1995).

Species richness and diversity in each quadrat were calculated for each of the three survey years. Species diversity was calculated as the inverse Simpson's diversity index (Hill number 3) in the vegan package (Oksanen et al. 2007) in R v3.0.2 (R Core Team 2019), since this is mostly commonly used and easier to interpret than the Simpson's index (Morris et al. 2014). Species which are designated as positive indicator species for CG2 grasslands in the UK are of particular relevance for assessing stand quality at the site (Appendix Table D.5) and were thus assessed for their richness and diversity (Common Standards Monitoring (JNCC 2004)).

To test for non-linear changes in species richness and diversity of all species and CG2 positive indicator species, I used generalized additive mixed models (GAMMs), a technique which is often used to detect non-linear patterns (Devictor et al. 2008, Polansky and Robbins 2013). Species richness of all species and CG2 indicator species were modelled using a Poisson error structure, whilst a Gaussian error structure was used for the diversity variables (Zuur et al. 2009). I included year as a smoother term and transect as a random effect using the "mgcv" package (Wood 2017) in R. To further examine whether vegetation change between 1970 and 2016 was non-linear, I also calculated the rates of change in species richness and diversity for 1970-1990 and 1990-2016. I compared the difference in time periods by pairing the change in species richness and diversity in 1970-1990 with the change in species richness and diversity in 1990-2016 using a Wilcoxon signed-rank test in R.

To examine whether soil properties over time were a consequence of N deposition, I assessed differences in the soil properties (LOI, pH, K, Mg, Ca, PO_4-P and N) over the three survey periods. I used general linear mixed models, with year as a fixed effect and transect as a random effect, using the lme4 package (Bates et al. 2014) in R. The significance of the year term was tested by creating a model with only the quadrat position nested in transect, and performing a likelihood ratio test of change in likelihood between models. The inclusion of a compound symmetry structure, which is often useful for the analysis of short time series (Zuur et al. 2009), had little effect on Akaike's Information Criterion (AIC), suggesting temporal autocorrelation was not an issue in my dataset; this error structure was not included in the final models.

To reveal if changes in vegetation reflected the soil status over time, I examined the correlation between the change in each of the soil properties with both the change in species richness and diversity. This was carried out for both time period comparisons (1970-1990 and 1990-2016) using Spearman's rank correlation, since the data were not normally distributed. In addition to examining species richness and diversity, I also assessed whether the soil properties combined to have a significant effect on the variation in species composition in 1970, 1990 and 2016, using a Redundancy Analysis (RDA). RDA was deemed the most appropriate technique, since a Detrended Correspondence Analysis revealed the gradient lengths were too short for a Canonical Correspondence Analysis (Ramette 2007). A subset of quadrats was used for this analysis, since not all quadrats had soil data associated with them. The significance of the constraining factors were analysed using ANOVA-like permutation tests (Oksanen et al. 2007).

To assess if signals of N deposition and grazing changes were evident through changes in the trait profile of the vegetation, I calculated community-weighted mean (CWM) traits (i.e. plot-level trait values weighted by species abundance) per quadrat for each survey year (Garnier et al. 2004) for plant height, SLA, grazing tolerance and the two Ellenberg indicators (N and R) to assess the potential impact of grazing pressure. I examined whether the CWM values of these traits differed between quadrats surveyed in 1970, 1990 and 2016, using general linear mixed models, with year as a fixed effect and transect as a random effect. The significance of the year term was tested as described above. The same methodology was used to determine changes in sward height in 1970, 1990 and 2016, modelled with a Gaussian distribution, since this is likely to be related to grazing pressure. I also assessed whether soil properties were associated with CWM Ellenberg N values using Spearman's rank correlation, since CWM Ellenberg N has been used to detect N deposition as a driver of vegetation change (Stevens et al. 2010, Emmett et al. 2011, Diekmann et al. 2014).

5.4. RESULTS

5.4.1. Vegetation change between 1970 and 2016

In total 83 vascular plant species were recorded during the three surveys (Appendix Table D.5). During the survey period, 22 of the 83 species showed an increasing trend in cover (27%), whilst 61 species had a decreasing trend (73%) between 1970 and 2016. Only three of the CG2 positive indicator species, *Helianthemum nummularium, Serratula tinctoria* and *Succisa pratensis* increased overall during between 1970 and 2016, whilst the other 12 species decreased (Appendix Table D.5). Species richness in 20 cm x 20 cm quadrats decreased from a mean ± 1 SE of 23.44 ± 0.36 in the 1970s to 20.97 ± 0.31 in 1990, to 14.43 ± 0.28 in 2016. Year as a smoother term was significant, suggesting a non-linear decline in species richness between the survey period ($p < 0.001$, $F = 115.6$, estimated degrees of freedom (edf) = 1.93) (Figure 5.2a). This was also evident when evaluating only CG2 positive indicator species ($p < 0.001$, $F = 28.4$, edf = 1.92) (Figure 5.2c). There were also significant non-linear declines in diversity in terms of all species ($p < 0.001$, $F = 165.2$, edf = 1.88) and CG2 indicators ($p < 0.001$, $F = 59.93$, edf = 1.97) between 1970 and 2016 (Figure 5.2b and 5.2d). The rate of species richness, diversity, indicator richness and indicator diversity change was significantly higher between 1990 and 2016, compared with between 1970 and 1990 (Table 5.2), which supports the GAMM results suggesting the rate of vegetation change between 1970 and 2016 was not linear. The species composition for the subset of quadrats in 1970 and 1990 in the RDA were more similar compared to that in 2016 (Figure 5.3), suggesting a larger shift in species composition in the final survey period.

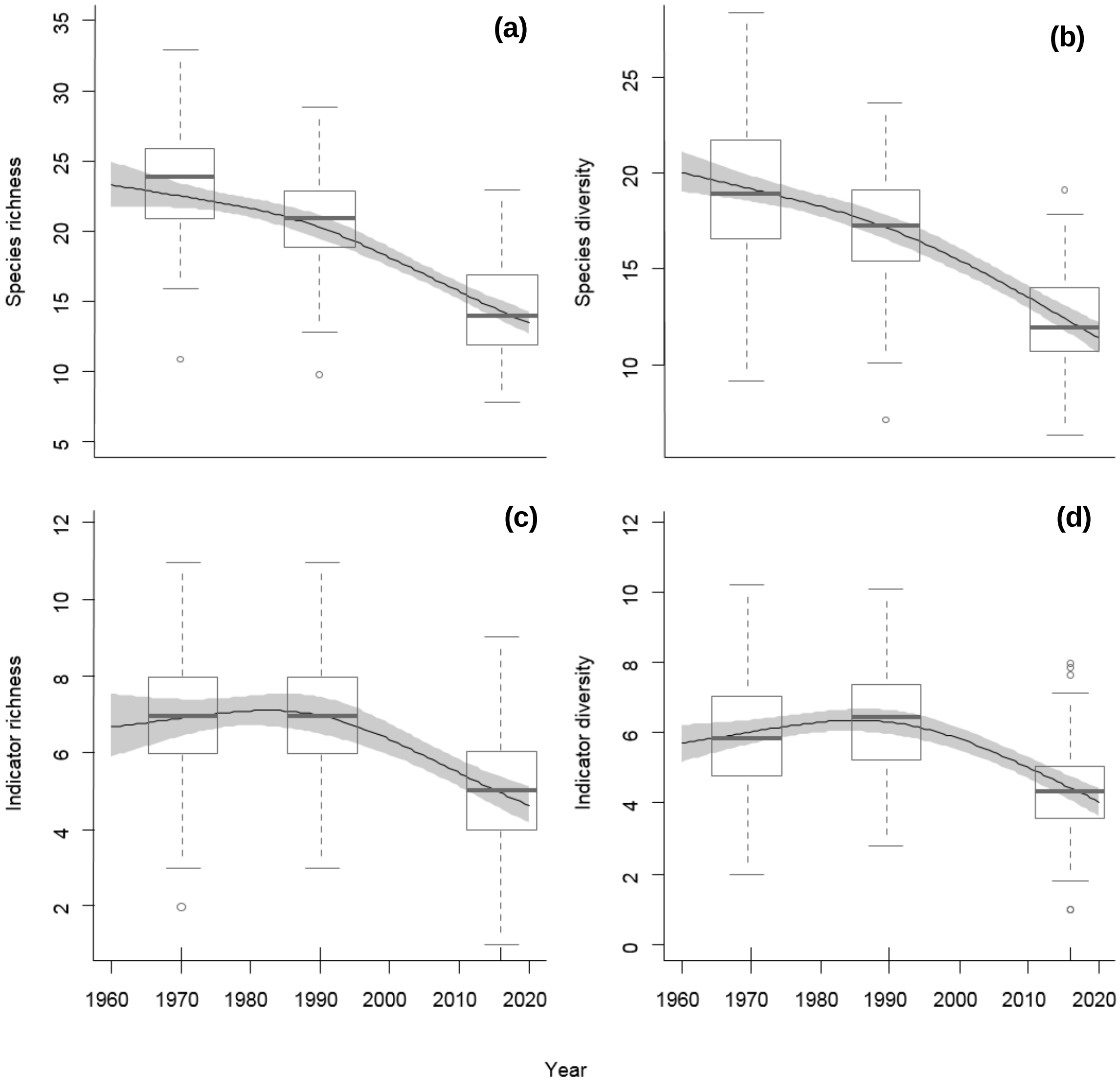

Figure 5.2 Boxplots of (a) species richness, (b) species diversity, (c) indicator richness and (d) indicator diversity, for 115 quadrats (20 cm x 20 cm) in 1970, 1990 and 2016 at Parsonage Down. Trend lines represent the fitted generalized additive mixed model, with ± SE indicated in grey.

Table 5.2 Average rate of change of species per year (± 1 SE) and Wilcoxon signed-rank test summary for species richness, indicator richness, diversity and indicator diversity between 1970-1990 and 1990-2016 at Parsonage Down.

	Average rate of change 1970-1990	± 1 SE	Average rate of change 1990-2016	± 1 SE	V	p
Species richness	-0.105	0.024	-0.232	0.017	4689	<0.0001
Indicator richness	0.007	0.012	-0.081	0.008	4754	<0.0001
Diversity	-0.098	0.024	-0.191	0.016	4366	0.004
Indicator diversity	0.015	0.011	-0.074	0.007	5108	<0.0001

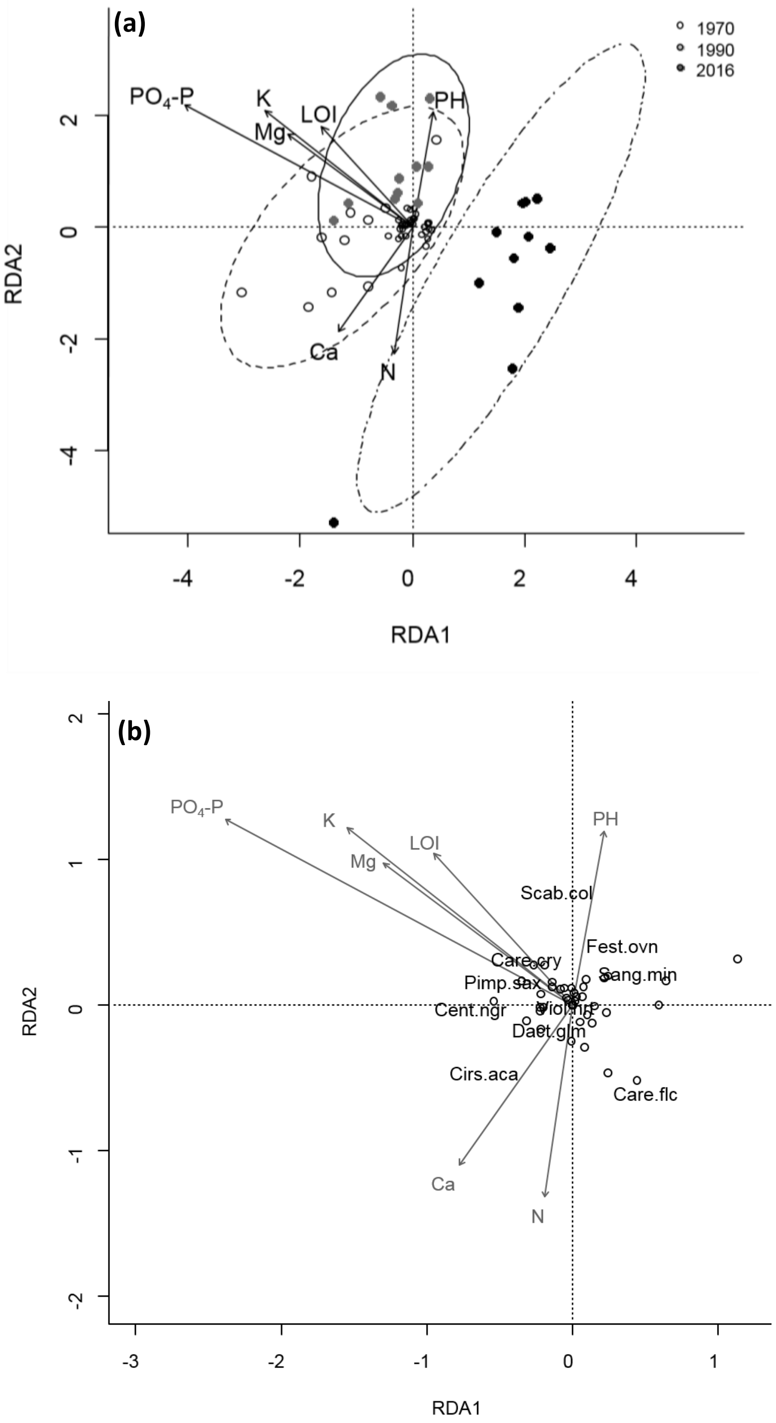

Figure 5.3 Redundancy analysis (RDA) plot based on 33 quadrats surveyed at Parsonage Down in 1970, 1990 and 2016. RDA1 and RDA2 have constrained Eigenvalues 8.48 and 4.56 respectively and explained 23.28% of the variation. Only soil phosphate (PO_4-P) was found to have a significant influence ($p = 0.001$). (a) Site scores. Quadrats surveyed in 1970 filled in white, while 1990 are represented in light-grey and dark-grey for 2016. Polygons enclose quadrats by date of survey, based on standard deviation of point scores. (b) Species scores. Only the most abundant species are labelled, in order of relative diversity (using the inverse Simpson index). Open circles indicate species whose names have been suppressed to declutter the ordination.

5.4.2. Soil properties

Chemical analysis of the soil revealed a statistically significant increase in total N across the three survey years ($p = 0.04$, X^2 (1) = 4.22) (Figure 5.4, Appendix Table D.2). Extractable Mg, on the other hand showed a significant decrease over the same period ($p = 0.003$, X^2 (1) = 8.85). Many of the other soil properties show more complex patterns of change (Figure 5.4), where an increase was evident between 1970 and 1990, followed by a decrease during 1990 and 2016. This was the case for pH ($p = 0.10$, X^2 (1) = 2.64), LOI ($p = 0.12$, X^2 (1) = 2.47), PO_4-P ($p < 0.001$, X^2 (1) = 30.32) and extractable K ($p = 0.002$, X^2 (1) = 9.99). Extractable Ca decreased between 1970 and 1990, but increased during 1990 and 2016 ($p = 0.002$, X^2 (1) = 9.87).

5.4.3. Changes in vegetation and soil status

Between 1970 and 1990 a significant negative correlation was found between changes in soil total N and species diversity (Table 5.3). In the later time period, soil K change was significantly negatively correlated with changes in both species richness and diversity, whereby small losses in Soil K were associated with a decrease in richness and diversity, however large losses led to an increase. The shift in composition from 1970 and 1990 to 2016 appears to be associated with a negative relationship with soil PO_4-P, Mg, K and LOI, though the ANOVA-like permutation test suggested that only soil phosphate had a significant influence (Figure 5.3a, Appendix Table D.6). *Carex flacca* was the only species to be located in the bottom right-hand quadrant associated with a lower soil PO_4-P, Mg, K and LOI (Figure 5.3b).

5.4.4. Trait profile

Several significant trends in community-weighted mean traits were identified between 1970 and 2016 (Figure 5.5). There was an increasing trend towards taller plant species between 1970 and 2016 ($p < 0.001$, X^2 (1) = 58.37), whilst the weighted-average SLA decreased during the same period ($p < 0.001$, X^2 (1) = 40.19). Grazing tolerance was greater in 1970 compared with 1990 and 2016 ($p < 0.001$, X^2 (1) = 13.98). Ellenberg N declined significantly ($p < 0.001$, X^2 (1) = 32.60), whilst Ellenberg R values remained consistent across the years, with a slight decrease in 2016, which was not significant ($p = 0.13$, X^2 (1) = 2.26). Ellenberg N was significantly correlated with soil pH (r_s = -0.38, p = 0.028) and Ca (r_s = 0.37, p = 0.035). No association was detected with Ellenberg N and soil N (r_s = 0.02, p = 0.931), PO_4-P (r_s = -0.05, p = 0.776), K (r_s = -0.05, p = 0.772), Mg (r_s = -0.05, p = 0.779) or LOI (r_s = 0.11, p = 0.546).

The sward height in 2016 (12.94 ± 0.47 cm) had increased considerably from 3.63 ± 0.09 cm in the 1970s and 1.99 ± 0.05 cm in 1990 ($p < 0.001$, X^2 (1) = 239.92), which appears to be consistent with the qualitative records obtained for grazing management at Parsonage Down between 1930 and 2011 (Table 5.1). The records show a decline in the number of cattle and sheep, suggesting a reduction in grazing pressure.

Table 5.3 Spearman rank correlations between changes in each soil property (pH, PO_4-P, N, K, Ca, Mg, LOI) with changes species richness and species diversity between 1970-1990 and 1990-2016 (n=33). P values <0.05 are indicated in bold.

		Species richness		Species diversity	
	Soil property	r_s	p	r_s	p
1970-1990	pH	-0.107	0.754	0.032	0.926
	PO_4-P	-0.251	0.457	-0.118	0.734
	N	-0.474	0.141	**-0.716**	**0.013**
	K	-0.105	0.759	-0.264	0.435
	Ca	-0.337	0.311	-0.481	0.137
	Mg	0.214	0.527	0.282	0.402
	LOI	-0.424	0.194	-0.609	0.052
1990-2016	pH	-0.14	0.682	-0.121	0.723
	PO_4-P	0.1	0.776	0.036	0.924
	N	0.209	0.539	0.055	0.882
	K	**-0.764**	**0.009**	**-0.836**	**0.002**
	Ca	0.218	0.521	-0.055	0.882
	Mg	-0.181	0.595	-0.163	0.634
	LOI	0.518	0.107	0.491	0.129

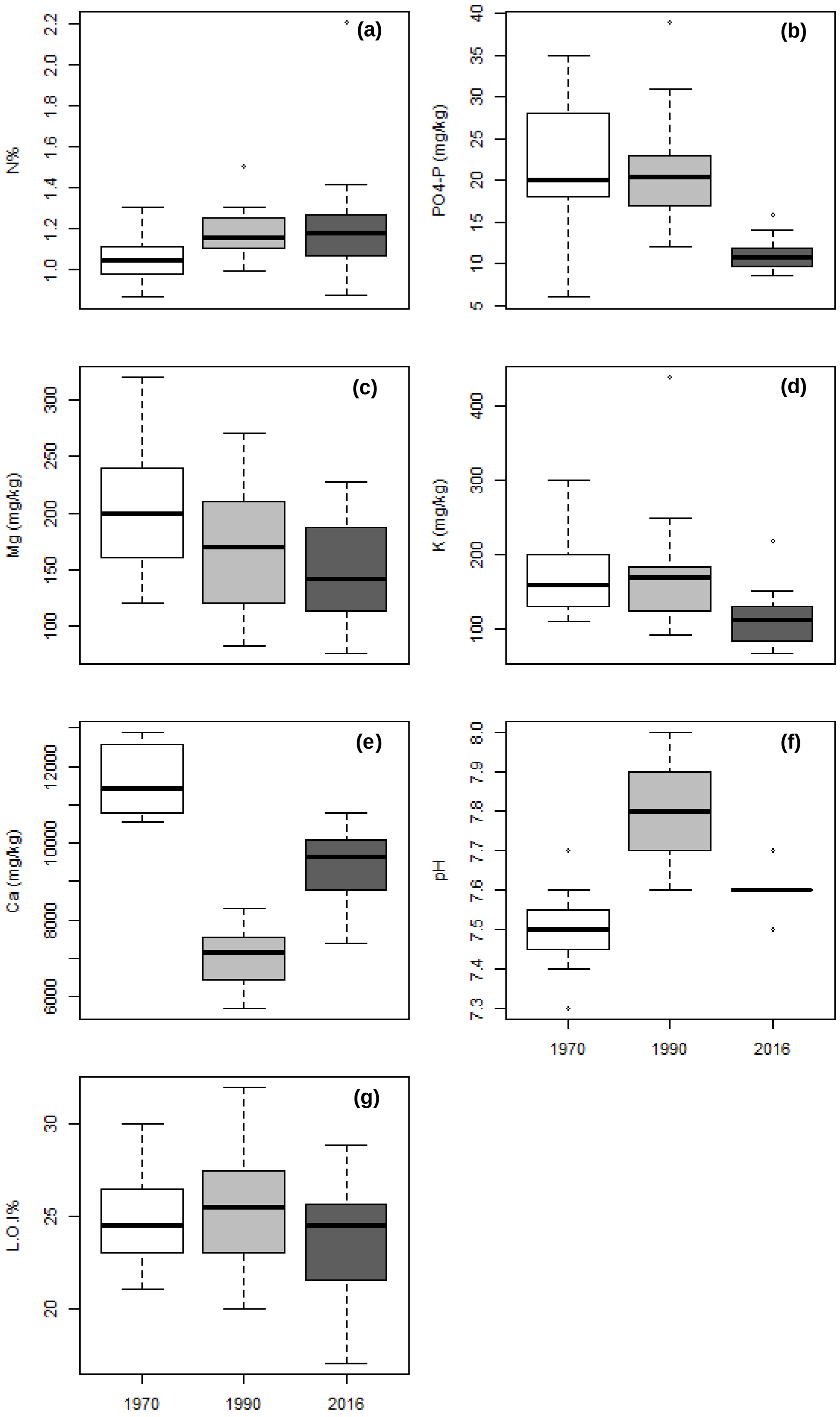

Figure 5.4 Boxplots of soil (a) total nitrogen, (b) PO_4-P, (c) Extractable Mg, (d) Extractable K, (e) Extractable Ca, (f) pH and (g) LOI from soil samples collected at Parsonage Down in 1970 (white), 1990 (light-grey) and 2016 (dark-grey).

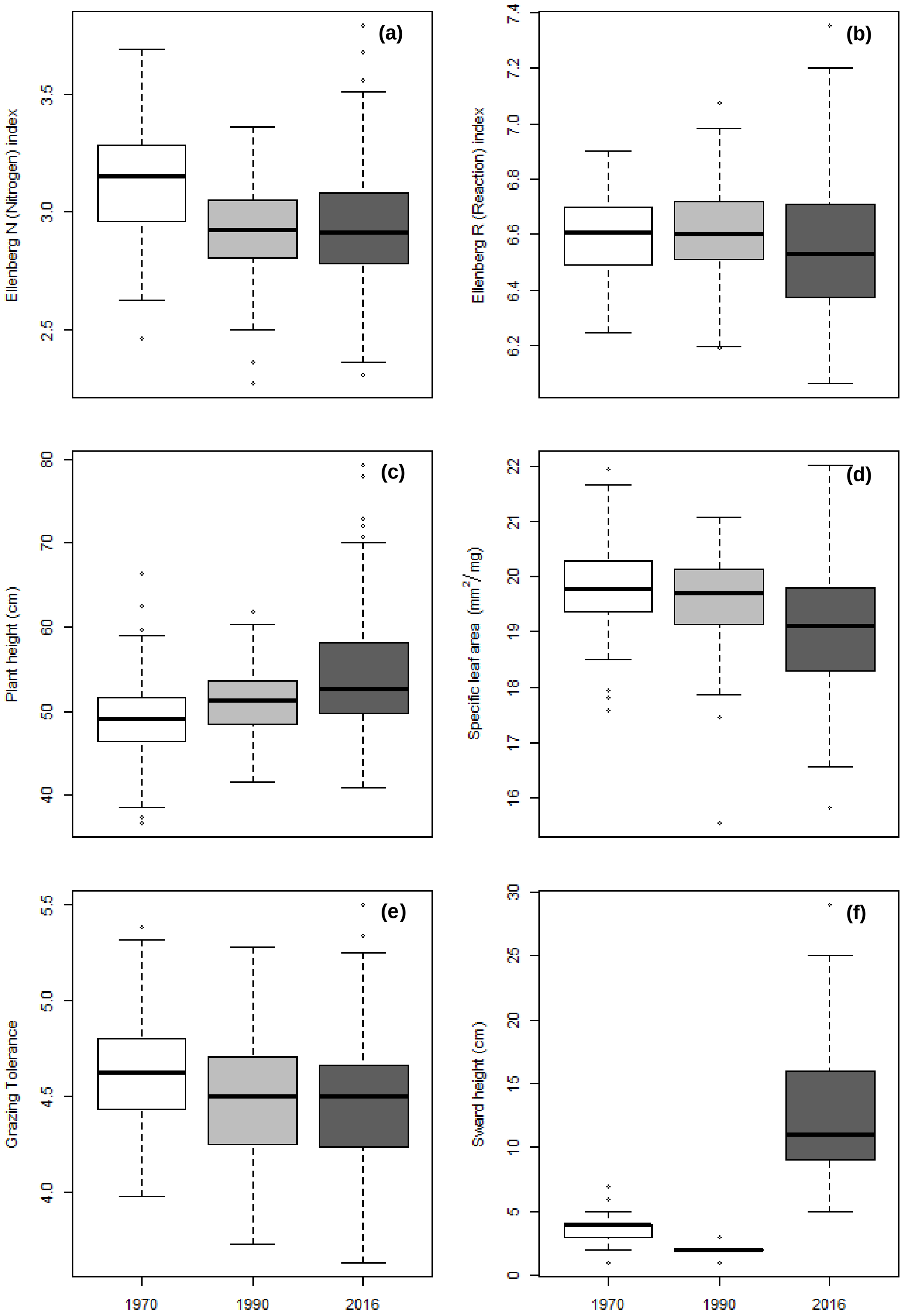

Figure 5.5 Boxplots of community-weighted traits in 1970 (white), 1990 (light-grey) and 2016 (dark-grey) at Parsonage Down; (a) Ellenberg Nitrogen (N) and (b) Ellenberg Reaction (R), (c) plant height, (d) specific leaf area, (e) grazing tolerance and (f) field-measured sward height.

5.5. DISCUSSION

5.5.1. Vegetation change between 1970 and 2016

Analysis of long-term changes in vegetation is limited, with very few studies evaluating multiple time points over nearly 50 years, with driver information (Newton et al. 2012, Diekmann et al. 2014, Stroh et al. 2017). This study has provided a rare opportunity to re-examine detailed transects, with driver data from multiple time periods. Although the analysis of re-survey data is commonly associated with some uncertainty, I have followed recommendations suggested by Verheyen et al. (2018) to increase the precision and strength of the inferences drawn from my study. This includes re-surveying a large number of plots, ensuring that transects were accurately relocated, having a team of well-trained surveyors (including one that was involved with the original survey) and by having a hypothesis-driven trait-based approach.

The analysis conducted in this study revealed a shift in species composition over the last 46 years. The shift was also associated with a non-linear loss in species richness and diversity, as hypothesised. This trend was also evident when examining just positive indicator species, which suggests that the quality of the vegetation at Parsonage Down is less favourable compared to that in the 1970s. Shifts in species composition in calcareous grasslands across the UK (Bennie et al. 2006, Newton et al. 2012) and Europe (Diekmann et al. 2014) have also been identified, whilst Stevens et al. (2016) also highlighted significant decreases in species richness and diversity in calcareous grasslands in the Sheffield region. This study, for the first time, was able to contrast the rate of change between two time periods. This rate was significantly higher between 1990 and 2016, compared with 1970 and 1990, suggesting change during the whole period was non-linear. This was further supported by the fitted GAMMs, which show a rapid decline in the species richness and diversity of indicator species in the latter time period. The trend line appears more linear for the species richness and diversity of all species, however the decline is more rapid in the 1990-2016 period and the significance of year as a smoother term also suggests the trend is non-linear, though caution must be taken when evaluating the P values alone (Zuur and Ieno 2016).

The increased rate of species richness and diversity loss between 1990 and 2016 coincides with a decline in grazing pressure at Parsonage Down. A sufficient grazing pressure is required to prevent the dominance of coarse grasses, allowing smaller forbs to flourish, thus a reduction in grazing may lead to the decline of these smaller species, and hence a loss of species richness and diversity. The grazing information provided in Table 5.1 suggests that the numbers of cattle and sheep grazing at Parsonage Down had decreased during the study period and there was a significant change from cattle over-wintering on the site during earlier years, to being taken off the site during winter. The patterns of grazing routines are also important; for instance at Parsonage Down, cattle favour the area where supplementary feeding was provided in the past, then they use the grassland close to trees when shelter is required (S. Hope 2017, Reserve Manager, pers. comm.). Thus, the location where the transects were recorded is currently grazed much later on in the season, once other areas have already been grazed down, allowing the sward to grow higher in this area. The height of the sward can also be used to represent grazing pressure (van den Berg et al. 2011). At Parsonage Down the sward height increased significantly over the time series, suggesting a reduction in grazing pressure, particularly during the latter time period, although it is important to consider that the wet spring and summer experienced in 2016 would have also contributed to this. Weather fluctuations are an important consideration when assessing vegetation change. The average temperature and total precipitation remained largely consistent between 1961 and 2015 at Parsonage Down (Appendix Figure D.7) and where larger fluctuations did occur (e.g. 1976, 1983 for rainfall), these did not correspond with my survey periods (1970 and 1990).

5.5.2. Soil properties

Significant changes in soil properties were identified over the survey period at Parsonage Down. The findings show a significant increase in soil total N content between 1970 and 2016, which is a signal often associated with N deposition (Zhang and Han 2012). The results also revealed significant declines in two of the base cations, Mg and K, which are released to buffer against N-induced soil acidification, providing further evidence for N deposition as a potential driver (Bowman et al. 2008, Horswill et al. 2008). This supports my second hypothesis where increases in soil N and declines in base cations have occurred as a consequence of N deposition.

Large declines in base cations were also detected in an experimental N deposition study in both acid and calcareous grassland in England (Phoenix et al. 2012), whilst Clark et al. (2007) used structural equation modelling to find species loss was higher with a lower soil cation exchange capacity (greater potential for acidification and loss of nutrient cations) using results from 23 N addition experiments across North America. The inconsistent trend demonstrated by pH over the study period has been observed in other research (Phoenix et al. 2012). Rowe et al. (2017) suggest that pH as a metric of N pollution and recovery is weakened by the impacts of historical sulphur deposition, which caused widespread and persistent acidification. Soil pH has increased in some areas due to the decline in sulphur deposition after the 1970s, however this is believed to have affected the N cycle. Soil phosphate remained consistent in 1970 and 1990, but declined significantly in 2016. Insufficient phosphate can lessen the effects of N deposition, which may explain why the impact of N deposition on the vegetation in this study was detected between 1970 and 1990 (see below). It is possible that grazing may have also contributed towards changes in the soil, however contrasting results are often reported in the literature. For instance, Bullock et al. (2001) found NO_3-N increased with winter grazing and heavier summer grazing, whilst Epelde et al. (2017) reported no effect of grazing on soil nutrient chemical parameters. Since grazing was kept largely consistent between 1970 and 1990 at Parsonage Down (Table 5.1), grazing is unlikely to have affected the soil during this period.

5.5.3. Changes in vegetation and soil status

To examine whether the soil changes evident in this study affected the vegetation, I assessed correlations between changes in each soil property and species richness and diversity between 1970-1990 and 1990-2016. Soil total N was significantly associated with a decline in species diversity in 1970 and 1990, suggesting that N deposition may have been a significant driver of vegetation change during this period, thus supporting my hypotheses. This coincides with the increasing period for total N in Figure 5.1. Declines in species diversity associated with increasing deposition of atmospheric nitrogen were also reported by van den Berg et al. (2011). They analysed 106 plots in nature reserves on calcareous grassland sites in the UK and identified a decrease in species diversity with high rates of N deposition. The results also suggest that even with consistent grazing management (Table 5.1), which occurred through 1970 and 1990, adverse effects of N deposition may still occur, as suggested by van den Berg et al. (2011). In the later survey period, a small decline in soil K was associated with a decrease in both species richness and diversity, whilst large declines were associated with an increase. Moderately high levels of potassium have been found to be associated with high levels of species diversity (Janssens et al. 1998), which may explain why a small loss in soil K led to a decline in species diversity at Parsonage Down, however this does not explain the increase in species diversity associated with a large decline in soil K in this study. Janssens et al. (1998) observed that the maximum species number is observed when the potassium content is 20 mg/100 g, which corresponds closer to the average potassium content recorded in this study in 1970 (17 mg/ 100 g) and 1990 (17 mg/100g) compared with 2016 (11 mg/ 100g), where species diversity was the lowest. Other studies, however, have found no impact of soil nutrients such as P and K on species richness and diversity (Bullock et al. 2001, Huber et al. 2017). A report by Wilson and Wheeler (2016) revealed higher potassium levels for sheep-grazed vegetation compared with mown, pony-grazed or unmanaged vegetation. During 1990 and 2016, the number of sheep grazing at Parsonage Down decreased (Table 5.1), which may therefore be related to the decline in potassium.

Although soil total N was associated with species diversity, the analysis revealed no significant influence on species composition, in contrast to Diekmann et al. (2014). Phosphate was the only soil parameter to significantly influence species composition at Parsonage Down, with the greatest shift apparent in 2016 associated with a decline in phosphate. *Carex flacca* was also related with this shift, which may be because *Carex flacca* has the potential to grow dauciform roots in areas of low phosphate (Davies et al. 1973, Shane et al. 2005), thus is able to perform well where phosphate is limited. The location of *Carex flacca* on the RDA plot (Figure 5.3) could also be linked to the lower grazing pressure experienced in 2016, since *Carex flacca* is fairly persistent in ungrazed areas and is also predicted to be less palatable (Grime et al. 2007).

5.5.4. Trait profiles as indicators of drivers of change

The increased fertility indicated by elevated Ellenberg N is often used to represent the effects of atmospheric N deposition on plant communities. The findings show a significant decline in community-weighted mean Ellenberg N values over time, which would suggest eutrophication is not one of the main factors responsible for the vegetation change evident at Parsonage Down. This is inconsistent with other studies reporting increases in Ellenberg N which have been attributed to increasing N deposition (Bennie et al. 2006, Keith et al. 2009, Newton et al. 2012). Others argue that Ellenberg N is unlikely to be an accurate predictor of the response to increasing N deposition. Wilson et al. (1995) found certain forb species, including *Thymus polytrichus, Scabiosa columbaria* and *Filipendula vulgaris* (all low Ellenberg N values) responded positively to N supply, suggesting Ellenberg N is not a reliable measure of a species' ability to compete under conditions of high N inputs. This supports the findings in this study, where evidence of N deposition through soil status changes, associated with species diversity declines between 1970 and 1990, is not reflected through the Ellenberg N CWM indicator. Stevens et al. (2010) also found no change in Ellenberg N. Furthermore, no association between Ellenberg N and soil N was revealed, instead Ellenberg N was found to increase significantly with a lower pH and a greater Ca content. Diekmann (2003) reported similar results, supporting the idea that nitrogen values would be better referred to as “productivity values”. No significant changes in Ellenberg R were detected over time in this study, which suggests that eutrophication, rather than soil acidification contributed towards the vegetation change associated with nitrogen deposition. This contrasts with Stevens et al. (2010) who identified soil acidification as the contributing factor for calcifuge grasslands across the UK.

Grazing management is known to have a significant effect on grassland species composition (Wallis de Vries et al. 2002). The analysis revealed a significant shift over time towards a community with a greater share of taller species (Figure 5.5a). Taller species can outcompete low growing species through competition for light, which can lead to a decline in species richness (Jacquemyn et al. 2003, Walker et al. 2009), as found in this study. Walker and Pinches (2011) found that negative population trends in *Pulsatilla vulgaris*, increased sward height and increased cover of *Bromopsis erectus* were related to a decrease in grazing pressure. *Bromopsis erectus* had established in around 17% of the Parsonage Down quadrats in 2016, where in 1970 and 1990 there was no record of the species (Appendix Table D.5). *Bromopsis erectus* is known to be a dominant species, with greater shoot thrust

(Campbell et al. 1992), which can restrict the growth of surrounding species. This coincides with the finding of more taller species in the community and may explain why smaller species such as *Euphrasia nemorosa*, *Campanula glomerata* and *Prunella vulgaris* decreased significantly between 1990 and 2016 (Appendix Table D.5). Species with smaller SLA values increasingly dominated the sward between 1970 and 2016. This maybe partly driven by the large increase in B. erectus in 2016, as previously mentioned which has a low SLA. *Lolium perenne* was another grass which had established in 35% of plots in 2016, despite being absent in the 1970s (Appendix Table D.5). This was most likely introduced from the supplementary feeding which occurred on the Down, which was stopped in 2003. The results also show a decreasing trend in grazing tolerance within the vegetation community, which provides further support for reduced grazing pressure, although unexpectedly the greatest difference in grazing tolerance occurred between 1970 and 1990, rather than 1990 and 2016 as suggested by the sward height and management information.

Many of the traits used to indicate grazing pressure as a driver are also used to detect N deposition. For instance, dominance by taller species is typical of competitive species in nutrient rich situations (Emmett et al. 2011). However, since signs of N deposition detected in the soil and its influence on species diversity was only evident for 1970-1990, this may suggest that the changes evident in the vegetation between 1990 and 2016 are largely attributable to grazing management. Although, Parsonage Down is only a single nature reserve, similar conclusions have been reported in other recent long-term resurvey studies which are within close proximity to Parsonage Down over similar time periods (Stroh et al. 2017, Hawes et al. 2018) and across the rest of the UK and Europe (Diekmann et al. 2019). Stroh et al. (2017) concluded that changes in lowland calcareous grassland were probably due to adjustments to grazing regimes, particularly regarding the fluctuations in timing and duration of livestock grazing. Similar conclusions were made by Hawes (2015) who reported no significant increase in total nitrogen, and concluded that vegetation changes were largely due to grazing. Furthermore, many argue that grazing management has a greater impact on species composition compared with N deposition (Wilson et al. 1995, Jacquemyn et al. 2003). This may mean that N deposition was still contributing to vegetation change in the later period since it accumulates in the soil, but the majority of change was caused by differences in grazing management. This is further supported by that fact that the rate of vegetation change was apparently greater in 1990-2016 compared with 1970-1990. Alternatively, the more intensive grazing management in the earlier time period may have helped mitigate the full impacts of N deposition.

5.6. CONCLUSIONS

This study has revealed a shift in species composition, combined with declines in species richness and diversity between 1970 and 2016 at Parsonage Down, with the greatest rates of change occurring between 1990 and 2016. There is some evidence that N deposition contributed towards these community changes between 1970 and 1990, as indicated by an increase in soil %N and the associated decline in species diversity. However, the evidence also suggests that vegetation change during 1990 and 2016 was largely attributable to a decline in grazing pressure, as indicated by an increase in taller species, decrease in grazing tolerance and reported grazing management changes. It is often difficult to dis-entangle grazing pressure and N deposition as drivers of change (Wilson et al. 1995, Clark et al. 2007), since vegetation often responds similarly to both drivers (Stevens et al. 2016, Stroh et al. 2017). However, as this study benefits from assessing multiple time periods, and a time series of soil analyses, it provides the first evidence of differential influences of N deposition and grazing pressure impacting on vegetation change during different time periods.

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CHAPTER 6

Responses of calcareous grassland plant communities to changed seasonal grazing management: results of a 31 year study

See: Ridding, L.E., Bullock, J.M., Walker, K. J., Bealey, C. and Pywell, R.F., 2021. Responses of calcareous grassland plant communities to changed seasonal grazing management: results of a 31 year study. *Journal for Nature Conservation*, 62 (August), 126026 https://eprints.bournemouth.ac.uk/35843/

CHAPTER 7

DISCUSSION AND CONCLUSIONS

This final chapter summarises the major findings of this thesis with respect to the three research questions outlined in Chapter 1. The results are subsequently integrated across all chapters and their wider implications are discussed. The final sections critically evaluate the research undertaken and explore ideas for further investigation, before summarising the key messages resulting from this thesis.

7.1. MAJOR FINDINGS

The destruction and degradation of habitats are major drivers of biodiversity decline globally. However, the spatio-temporal dynamics of such changes are not fully understood, yet this information is critical for predicting future changes and employing conservation management to halt the decline in biodiversity. Using southern England as a case study, this thesis examined drivers of habitat loss and quality using long-term data with more than two snapshots in time. The following sections discuss the main findings in respect to the research questions set out in Chapter 1; (i) what are the spatio-temporal patterns and drivers of habitat loss? (ii) does habitat loss lead to extinction debts across a range of habitat types? (iii) what are the temporal patterns and drivers of vegetation change in calcareous grasslands?

7.1.1. Spatio-temporal patterns and drivers of habitat loss

This thesis provides further evidence of the extensive loss of semi-natural habitats in the UK during the twentieth century (Fuller 1987, Ridding et al. 2015). To date, there has been limited knowledge of how these losses have played out over time and the drivers responsible. Chapters 2 and 3 address this knowledge gap by generating a novel habitat time-series dataset and a land use/land cover (LULC) map time-series, respectively. This has enabled important aspects of disturbance theory to be identified and compared amongst different habitats spatially and temporally, including their extent and magnitude. The magnitude of loss was greatest for neutral grassland, followed by calcareous grassland, though the temporal patterns of these losses were similar. The greatest losses occurred between 1950 and 1980 and were largely driven by agricultural intensification, as seen across the rest of Europe (Plieninger et al. 2016, Aune et al. 2018). The decline in these habitats and in the majority of other semi-natural habitats (acid grassland and heathland) examined was non-linear between 1930 and 2015, with the number of habitat patches lost declining after the 1980s. This is consistent with Bibby (2009), who reported that the rate of land use change in the UK was slower between 1983 and 2008 compared with the post-war period up to the 1970s. In addition to agricultural intensification, other drivers such as afforestation and urbanisation also led to the loss of habitat patches between 1930 and 2015, but to a lesser extent. Heathlands were an exception to this, with many patches lost to coniferous woodland and urban areas. This largely occurred in the south-east of the county, whilst large areas of neutral grassland (predominately located in the north-west) were converted to improved grassland. Calcareous grassland which ran south-west to north-east of the county tended to be lost to arable land (Chapter 3). The number of semi-natural habitat patches continued to decline after 1980 despite there being so little remaining, which suggests that urbanisation, afforestation and agricultural improvement are still important drivers of change. These findings support the idea that habitat destruction, through land cover change is still a key driver of biodiversity loss.

7.1.2. Extinction debts across a range of habitat types

This thesis reveals that habitat loss led to extinction debts in plant communities across three different habitat types; calcareous grassland, heathland and broadleaved woodland (Chapter 4). This is the first time that more than one habitat type has been examined within the same study system, which allowed for comparisons between the different degradation histories determined in Chapter 2. Furthermore, this is the first time that three extinction debt methods have been compared and contrasted within the same study system, thus addressing the key knowledge gap identified by Kuussaari et al. (2009). The conclusions from the three different extinction debt methods were inconsistent. Calcareous grassland, which underwent severe degradation, was the only habitat for which an extinction debt was suggested by all three methods. The method which required information on past species richness was the only one to suggest an extinction debt across all three habitat types. Previous studies which have compared extinction debt methods only considered two, which did not include this more data intensive method. These previous studies reported consistent findings between the two methods (Guardiola et al. 2013, Soga and Koike 2013). The research presented in Chapter 4, which also compares the most data intensive method therefore contributes new evidence regarding the conclusions of such studies. This research suggests that the inclusion of past species richness data is critical when evaluating the presence of extinction debts, particularly when the habitat degradation is less severe. This finding has important implications for the reporting of extinction debt studies in the literature and for employing conservation action (see section 7.3.)

7.1.3. Temporal patterns and drivers of vegetation change in calcareous grasslands

Chapter 5 and 6 extended and analysed long-term studies of vegetation change in an important conservation habitat; calcareous grassland at two nationally important sites in southern England. However, despite the close proximity of the calcareous grassland sites, the conclusions of both chapters differed. Chapter 5, which examined vegetation change in 1970, 1990 and 2016 at Parsonage Down NNR identified a significant decline in species richness, diversity and a shift in composition over time. On the other hand, Chapter 6, which evaluated change across multiple time periods between 1979 and 2010 at Martin Down NNR, showed that the vegetation community has remained largely consistent between these time periods. The results presented in Chapter 5 are more consistent with those reported in the literature, which also document shifts in communities and declines in species richness and diversity (Newton et al. 2012, Diekmann et al. 2019). Although the sites examined in Chapter 5 and 6 cannot be directly compared due to other influencing factors such as soil properties and topography, one of the key differences is the grazing management employed at each site. Parsonage Down is more traditionally managed by so-called ‘set stocking’ of livestock, where cattle and sheep graze across large areas of the site. In contrast, Martin Down is common land where permanent fencing is not permitted. Since the 1970s, this grassland has been grazed by erecting small, temporary pennings using electric fencing. These pennings are intensively grazed by large numbers of sheep for short periods, so-called “mob grazing”. This latter approach appears to less common on reserves across the UK, the notable exception being Salisbury Plain where the requirements of military training prevents permanent fencing (Woodcock et al. 2005). At Parsonage Down the reduction in grazing pressure over time was attributed to one of the key drivers of vegetation change between 1990 and 2016. This period saw a greater decline in species richness and diversity compared with 1970 and 1990. Conversely, Martin Down which experienced a dramatic shift in grazing management (from all year round to predominately autumn and winter) did not seem to impact the vegetation community dramatically. This raises interesting questions about whether mob grazing could help to mitigate the impacts of reduced cattle/sheep and shifts in seasonal grazing, with the latter most likely brought about with the introduction of the Lowland Grassland Management Handbook (Crofts and Jefferson 1999). However, more research is required comparing traditional grazing with mob grazing through a controlled experiment before any reliable conclusions can be determined.

Chapter 5 also provided a unique opportunity to assess the impact of other potential drivers of vegetation change such as nitrogen deposition. This was made possible through the analysis of soil samples at three time periods which is rare alongside vegetation data. This is particularly important because the impact of nitrogen deposition on calcareous grassland is unclear, with some studies reporting effects on vegetation (van den Berg et al. 2011, Diekmann et al. 2014) and others reporting no effects (Maskell et al. 2010). Chapter 5 found that nitrogen deposition contributed towards vegetation change between 1970 and 1990 at Parsonage Down. The findings are an important step towards separating the entangled relationship between nitrogen deposition and grazing management (Wilson et al. 1995, Jacquemyn et al. 2003), where in Chapter 5 I concluded that both drivers were influencing vegetation change during different time periods. This was only possible due to the additional time period (1990) that was available to analyse, which emphasises the importance of such long-term and detailed monitoring studies.

7.2. INTEGRATION ACROSS CHAPTERS

This thesis has a running theme of using long-term data across multiple time periods to assess both pulse (habitat destruction) and press (habitat degradation) disturbances over time. The findings across each chapter all highlight the importance of examining these two types of disturbances over more than two snapshots in time, and this enabled the patterns and drivers of these changes to be determined. This thesis has made an important contribution to quantifying temporal patterns in the extent and condition of important semi-natural habitats, as there is currently limited knowledge on the magnitude of losses at multiple time intervals in the UK. Often habitat loss is presumed to be linear over time, though this thesis revealed a non-linear loss for the majority of semi-natural habitat types. This non-linear pattern was also detected when assessing habitat degradation in Chapter 4, where the loss of species richness and diversity in calcareous grassland was greater between 1990 and 2016 compared with 1970 to 1990. These findings support the idea that both habitat and vegetation change are dynamic and emphasise the importance of evaluating change using more than two time points. Although the drivers of habitat loss are well established in the UK (Winn and Tierney 2011), this thesis has assessed the time periods in which the drivers were most influential and which habitats were most impacted by the respective driver. For instance, between 1930 and 1950 the majority of semi-natural grasslands were lost to agricultural intensification, whilst heathland within the same region was largely lost to conifer plantations (Chapter 2). The roles of multiple drivers of change during different time points was also evident in Chapter 5, where nitrogen deposition was considered a driver of vegetation change pre-1990, whereas a decline in grazing pressure was most likely more influential after this point. With data from only two time periods, such temporal patterns and drivers in habitat change cannot be determined accurately, whether assessing press or pulse disturbances, as done in this thesis.

Calcareous grassland was the only habitat type to be assessed across every chapter in this thesis, allowing detailed assessment of change in overall extent (pulse) and community composition (press) to be assessed. Calcareous grassland experienced some of the greatest losses over time in Dorset, second only to neutral grassland, with the greatest losses occurring between 1950 and 1980 due to agricultural intensification (Chapter 2). Chapter 3 revealed the spatial patterns of this loss, where calcareous grassland was largely lost to arable land in the region running south-west to north-east along the chalk ridge in Dorset. The patterns in calcareous grassland loss were important to understand for Chapter 4 when evaluating the three extinction debt methods. Even the two methods which were considered less robust, detected extinction debt in calcareous grassland, highlighting the dramatic degradation of this habitat. This was further evident when assessing vegetation change over time in Chapter 5, which revealed declines in species richness, diversity and shifts in species composition. Despite the dramatic loss and decline in the quality of calcareous grassland revealed by the long-term studies, the research undertaken also provides hope for the future of this habitat. Firstly, although Chapter 2 revealed a dramatic loss in calcareous grassland, the analysis also found that those that were protected through designation as a Site of Scientific Interest (SSSI) were more likely to remain as their original habitat (see section 7.3.). This is supported further by the results in Chapter 6, which show that despite a drastic change in grazing management, the vegetation community remained largely consistent over time, supporting the idea that this habitat is resistant to change. Finally, the detection of an extinction debt using every method in Chapter 4 provides greater certainty that an extinction debt is present in calcareous grassland. This means the habitat is under significant threat, but there is still time to employ conservation action to avoid paying off the extinction debt.

7.3. WIDER IMPLICATIONS

Recent initiatives, such as the Nature Recovery Network (DEFRA and Natural England 2020), seek to achieve landscape scale restoration and re-connection of semi-natural habitats across England. This makes the maintenance of remaining semi-natural habitats as critical as ever, particularly when so little remains, as evident in this thesis. The results from Chapter 2 show that where a semi-natural habitat was legally protected from damage through designation as a SSSI, the site was less likely to be lost compared with a site that was not protected. This suggests that statutory protection through designation was beneficial for conserving semi-natural habitats. Although evidence for the benefits of protected areas across the globe are variable (Clark et al. 2013, Spracklen et al. 2015), there are a number of other studies which support this idea (Geldmann et al. 2013, Riggio et al. 2019). This finding has important implications for policy in the UK, as it provides crucial evidence for the effectiveness of such protection and the need for this to continue in the future. Furthermore, the results also suggest that protecting additional areas of semi-natural habitats would be valuable for their retention in the future, which provides support for plans to increase protected land by 4% in the UK (DEFRA 2020).

In addition to the conservation of remaining semi-natural habitats, there are also opportunities to restore and re-create habitats which have been lost or degraded. The results from this thesis are particularly important for this, since they identify the location of lost habitats and thus reveal where future restoration activities might be targeted. This demonstrates the value of modelling change for the whole region (Chapter 3), in addition to the time-series dataset generated in Chapter 2. Chapter 4 highlighted the value of implementing restoration to avoid paying off the extinction debt, though extinction debts were only detected in all three habitats using the most data intensive method, as previously discussed. This is critical, because if an extinction debt is not thought to be present, the benefits of conservation action, such as restoration, are less clear. In particular, restoration to avoid paying the extinction debt would require planning to reverse the habitat and species loss around remaining patches. The findings in this thesis suggests that where possible, past species richness data should be considered for extinction debt analyses, particularly for those habitats which have experienced moderate degradation. This, and the studies at Parsonage Down and Martin Down, emphasise the value of long-term ecological monitoring to inform future conservation actions. Where past species richness data is unavailable and so only the other two methods can be employed, caution needs to be taken with these results and the decision for planning restoration, should not rest solely on these conclusions.

The restoration and re-creation of semi-natural habitats is becoming increasingly widespread across Europe and the UK (Kiehl et al. 2010, Rothero et al. 2020) and its importance is recognised globally as we commence the UN Decade on Ecosystem Restoration (2021-2030) (United Nations 2019). In the UK, considerable research has been undertaken on restoring or re-creating species-rich grasslands on agricultural soils (Pywell et al. 2002, Walker et al. 2004, Wagner et al. 2020). Agri-environment schemes have played a significant role in the restoration and re-creation of semi-natural habitats in the UK by providing farmers with financial incentives to make environmental improvements to their land (Critchley et al. 2004). With the UK’s departure from the European Union (EU) and consequently the EU’s Common Agricultural Policy, the UK has a unique opportunity to develop new policies which can enhance and increase the extent of semi-natural habitats. This is further supported by other policies including the UK Government's 25 Year Environment Plan which aims to expand and restore semi-natural habitats (DEFRA 2018).

Equally important as the restoration of semi-natural habitats such as calcareous grasslands, will be the conservation and improvement of existing remnant patches of this habitat through appropriate management. This will be vitally important if populations of associated invertebrate and bird species are to colonise these newly created grasslands. In Chapter 5, I reveal that a decline in grazing pressure is one of the key drivers of vegetation change. This is consistent with a number of other studies across the study system and the rest of the UK, which have revealed declines in grazing pressure, as well as shifts in the grazing season (Walker and Pinches 2011, Stroh et al. 2017, Hawes et al. 2018). The Lowland Grassland Management Handbook (Crofts and Jefferson 1999), which sets out the best practice management for habitats such as calcareous grassland, was first published in 1999. The results presented in this thesis and the widespread decline in the quality of calcareous grassland in the UK, indicated by losses in species richness, diversity and shifts in composition (Bennie et al. 2006, Newton et al. 2012, Stevens et al. 2016), suggests that the current grazing management advice needs to be revised. At a local level, the results of this thesis have led to important management decisions within Wiltshire. After presenting the findings from my thesis at several stakeholder meetings and more recently at the Natural England Chalk Grassland Management Summit (October 2020), the grazing management at some Wilshire NNRs is now being adjusted in response to the findings, including introducing grazing earlier in the year and grazing in additional seasons. Moreover, my research has highlighted the importance of ongoing monitoring of the impacts of changed grazing management on plant community composition.

7.4. CRITICAL EVALUATION OF RESEARCH

The following sections outline some of the caveats in the methods employed in this thesis. Where possible, I discuss how these have been minimised or how these could be addressed in future research.

7.4.1. Data availability

Although this thesis addresses a key knowledge gap regarding the use of long-term data across more than two snapshots in time, additional data is always more advantageous. This was particularly relevant for the chapters examining vegetation change in calcareous grassland (Chapter 5 & 6). In Chapter 5 data for only three time periods were available, which comprised the fewest time points assessed across all chapters in this thesis. Although it was possible to detect change in vegetation and associated drivers differed between 1970 and 1990 vs 1990 and 2016, additional time periods would have helped to identify the temporal patterns of this change even clearer. Specifically, it would have helped determine the impacts of inter-annual climate factors, for example droughts, on vegetation community responses. Chapter 6, in contrast, evaluated change using the greatest number of time periods used across all chapters. However, the vegetation quadrats were located across different vegetation community types, which were recorded at irregular intervals across the survey period. This made it more difficult to assess change across time, although I addressed these issues with careful use of statistics. Martin Down NNR, the site examined in Chapter 6, is now included within Natural England's Long Term Monitoring Network (discussed in section 7.5.2.), which will support the evaluation of vegetation change at this site in the future.

Another limitation encountered in chapters 2-4, was the spatial extent of the study region. Prior to 1974, Dorset was ca. 2500 km^2, since it excluded the urban areas of Bournemouth, Poole and Christchurch. These urban areas were not recorded within the Good (1937) survey, the framework I used to create the time-series dataset in Chapter 2, nor were the areas included within the adapted Dudley Stamp Map for Dorset (Hooftman and Bullock 2012), which I used to model the 1950 and 1980 maps in Chapter 3. Because this habitat information was missing from the baseline, I was unable to consider the full impact of urbanisation on semi-natural habitats in Dorset within this thesis. This is unfortunate since there is strong evidence that the expansion of Bournemouth, Poole and Christchurch have had a considerable detrimental effect on the extent and quality of lowland heathland habitats over time (Webb and Haskins 1980). This is particularly relevant since urbanisation is an important driver of biodiversity loss (McDonald et al. 2020, Olivier et al. 2020) which is expected to become increasingly important in the future (Seto et al. 2012), thus understanding this driver in the past would have been very useful for predicting future change. Although these urban areas were not considered in this thesis, I still identified urbanisation as a driver of habitat loss for calcareous grassland, fen, marsh and swamp and heathland, largely between 1930 and 1950 across Dorset, thus these patterns could still be used to infer habitat loss in more urbanised areas.

7.4.2. Data quality

The value of long-term data was discussed in Chapter 1, however there can be a number of disadvantages or difficulties associated with using such data. These points are highlighted in Table 7.1. Inconsistencies over time in relation to the survey interval, sampling method, observer and location were particularly relevant to this thesis. Caution needs to be taken with such results because errors associated with the sampling method, observers and relocation are important (Morrison 2016, Kapfer et al. 2017, Verheyen et al. 2018, Lisner and Lepš 2020). There have been several resurveys of the original Good (1937) survey which I utilise in Chapters 2, 3 and 4, including Horsfall (1981), Newton et al. (2012), Keith et al. (2009) and Diaz et al. (2013). The error associated with the relocation of these sites is likely to be less compared with navigating to a specific quadrat (e.g. Chapter 5 and 6), since the survey sites ranged between ca. 0.5 and 70 ha. Furthermore, Good (1937) provided detailed site descriptions and locations, allowing them to be relocated accurately. Although the resurveys were recorded by different surveyors, which is very common in such studies, these surveyors were all experts. In addition, only presence/absence data was recorded rather than the abundance of plant species, thus eliminating the variation which can occur with cover estimates (Milberg et al. 2008). Similarly, the resurveys undertaken by reserve managers and staff at Martin Down NNR, which I utilise in Chapter 6, were all recorded by experts. Some of the locations were also permanently marked between years, thereby decreasing the likelihood of pseudo-turnover, where species may be incorrectly recorded as extinct or colonising due to misplacement of the survey plot (Fischer and Stöcklin 1997). Where I undertook the resurvey (Chapter 5), I ensured that measures were taken to increase the precision of the study as suggested by Verheyen et al. (2018). Firstly, the observer error was reduced by having a surveyor who recorded in both the original survey and resurvey. Secondly the survey involved recording a large number of quadrats, thus increasing the likelihood of detecting real change in the community (Verheyen et al. 2018).

Finally, plots were accurately re-located using original survey maps and detailed descriptions. The location of these plots were recorded using a GPS accurate to ± 2 m in 2016, thus in the future these can be relocated with higher confidence.

The other limitation encountered in this thesis relates to the resolution of the data rather than the quality per se. For Chapter 3 and consequently Chapter 4 which uses the dataset from the preceding chapter, the information on habitat loss and land cover change was at a 100 m resolution. This is because the intermediate maps for Dorset produced in Chapter 3 used the InVEST Scenario Generator Rule-Based tool (Sharp et al. 2016), which required a balance of understanding detailed land cover change, but also maintaining a scale where driving factors, such as soil types, would be influential, as well as controlling the model run time and file sizes. The generated map time-series is useful for examining general patterns of change and has also been used to determine changes in ecosystem delivery over time (Watson et al. n.d.), however it is not suitable for fine-scale analysis. In Chapter 4 the map time-series was used to determine the amount of focal habitat within 1 km buffers. If a finer resolution was available, other connectivity indices (Hanski and Thomas 1994, Moilanen and Nieminen 2002) could have been incorporated into the extinction debt analysis instead of the amount of habitat area.

7.4.3. Modelling

There are a number of assumptions and caveats associated with the modelling employed in Chapter 3 to produce intermediate LULC maps for Dorset. Firstly, although the transition matrices were used to inform which LULC changes occurred within the different classes, the InVEST tool only allowed the percentage change input of LULC classes that increased over time, not those which decreased. Furthermore, the location of where these transitions had occurred was not factored into the tool. Including both of these factors would have improved the accuracy of the final map output. One of the major weaknesses of such tools is the omission of indirect factors which are often very influential on LULC change, such as political and economic drivers or land ownership (Bibby 2009). Future work will need to consider integrated modelling, where other socio-economic variables are considered (e.g. Schaldach et al. 2011).

Table 7.1 Advantages and disadvantages of long-term ecological data (Strayer et al. 1986, Magurran et al. 2010, Lindenmayer et al. 2012, Lohner and Dixon 2013, Verniest and Greulich 2019).

Advantages	Disadvantages
• Useful for providing a baseline against which current trends can be compared • Understanding environmental change and its impact on ecosystems. • Provides an opportunity to understand rare events • Understanding complex ecosystem phenomena that occur over prolonged periods • Allows slow ecological processes such as forest succession to be studied • Promotes multidisciplinary research • Useful data for developing and testing ecological theories • Important for education and connecting with the general public	• Expensive to run and maintain long-term experiments or survey programmes. • Inconsistencies in survey intervals, sampling method, observer and location. • Reliant on data-sharing or digitisation of historic records • No clear definition of "long-term" or uncertainty on "how long is long enough?" • As drivers change over time, forethought is required to have surveyed relevant drivers in the past

7.5 FURTHER RESEARCH

This thesis has identified several paths for further research, which largely falls within two key themes. Firstly, expanding this research both temporally and spatially, in order to understand ongoing and future threats, such as climate change. Secondly, the need for mitigating drivers of change through habitat management.

7.5.1. Continued monitoring and upscaling research

This thesis has highlighted the importance of assessing long-term change over multiple time periods. However, the monitoring of such change needs to continue in the future in order to understand emerging threats and ultimately to halt the decline in biodiversity. For this to be possible, datasets and surveys need to be produced and undertaken, respectively, at regular intervals in the future using consistent protocols to enable data integration. There are already promising signs this is beginning to happen. For example in the UK, the first land cover change product has been published, which assesses land cover change between 1990 and 2015 (Rowland et al. 2020). At the habitat scale, repeating vegetation surveys (and also for other taxa) through time is essential for identifying drivers of change and being able to respond quickly to address such changes. I plan to re-record the transect study at Parsonage Down NNR (Chapter 5), but there is also a permanent record of the study, openly stored on the Environmental Information Data Centre (EIDC) for others to use. This continued monitoring is as important as ever, because although the impact of drivers such as nitrogen deposition have reduced over time, other drivers such as climate change are becoming increasingly important (Basto et al. 2018, Mitchell et al. 2018, Löffler et al. 2019). The importance of understanding long-term habitat change has also led to the establishment of the Long Term Monitoring Network. Set up by Natural England in 2009, this network monitors weather, air quality, land management, vegetation, soil chemistry and communities and bird and butterfly populations at 37 sites across England (Natural England 2017). Martin Down NNR is part of this network, which provides a fantastic opportunity to expand the research undertaken in Chapter 6 to other sites in the future.

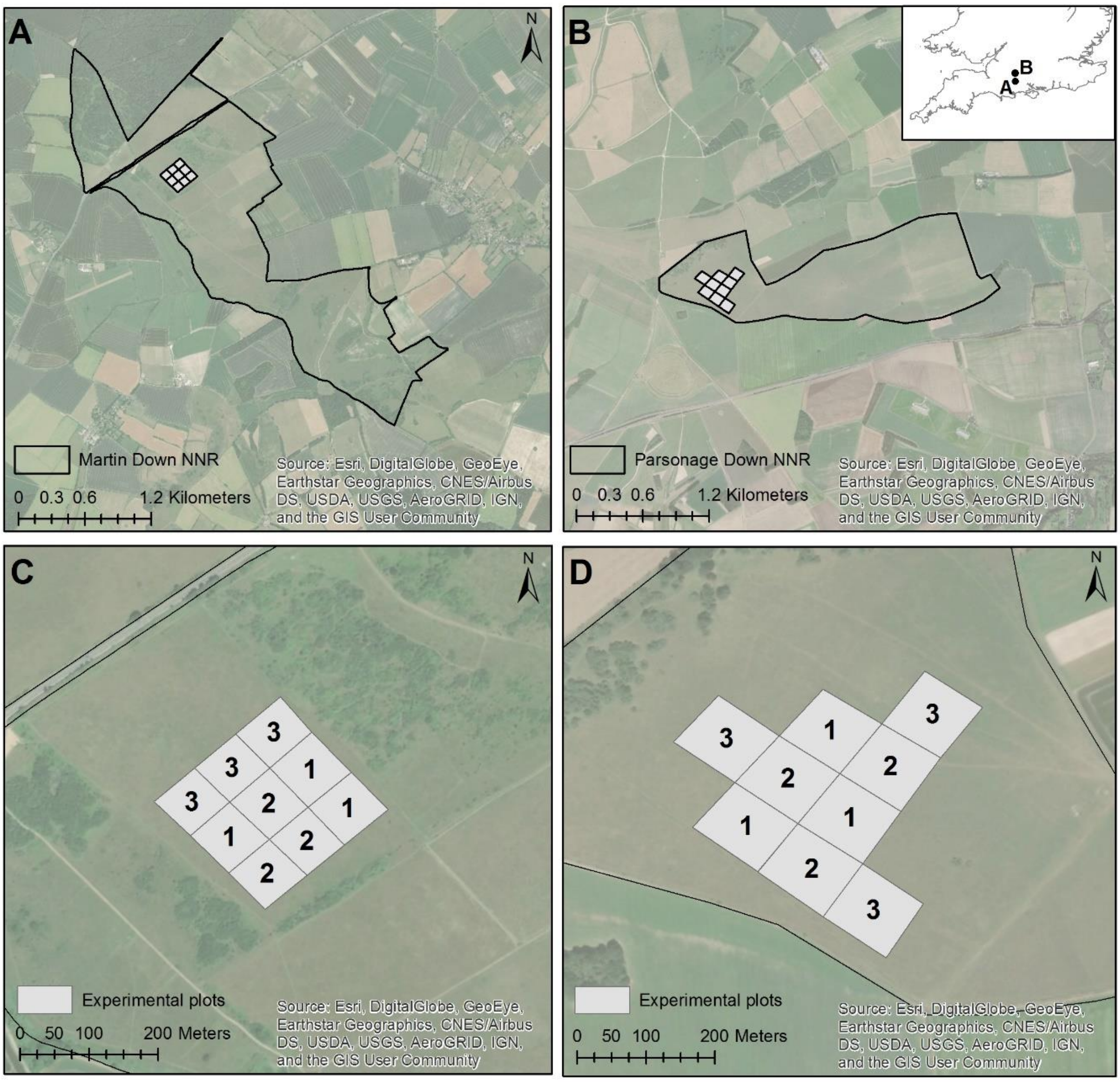
In Chapter 3 I used the InVEST Scenario Generator tool, to model historical landscapes in Dorset. Rather than back-casting as I performed, the tool was originally designed to explore future scenarios following engagement with stakeholders. There is therefore an opportunity to expand this research further by modelling potential future landscapes. This has already been carried out for Dorset using an alternative method, where two scenarios of agricultural expansion were compared with two scenarios of landscape-scale ecological restoration and the current situation (Newton et al. 2021). However, additional scenarios could be examined using the InVEST tool based on the trends in habitat change evident in Chapter 2.

As well as continuing the temporal aspect of long-term change, there is also a need to expand this research spatially. In this thesis I focus on southern England as a case study. However to increase our understanding of semi-natural habitat change this would ideally be expanded to the whole of the UK, where different drivers may be impacting on habitats in other regions. In Chapter 3, afforestation was a key driver of habitat loss in the south-east of Dorset, while agricultural intensification resulted in the loss of neutral grassland in the north and west of Dorset. Thus, across the whole of the UK, a range of spatial patterns in habitat loss and associated drivers are likely to exist. The assessment of vegetation change in calcareous grassland would also benefit from having additional data from sites across the UK, where other drivers such as climate, topography and landscape composition may play an important role.

Chapter 4 highlighted the importance of using past species richness data in extinction debt analyses, yet to date very few studies incorporate this (Cowlishaw 1999, MacHunter et al. 2006). There is a need to undertake more research using this more data intensive methods to gain a better understanding of the presence of extinction debts. There is also an opportunity to upscale research in extinction debt, beyond the comparison of methods and habitats as done in this thesis for the first time, by comparing such patterns across different countries. Additional factors should be included in a cross-country analysis, including management and topography. These additional factors considered across a wider study system may provide a useful insight into the differences in the degree of extinction debt detected, and consequently may help to inform restoration.

7.5.3. Addressing drivers of change

This thesis has addressed key knowledge gaps by assessing long-term habitat change across multiple time periods. The research has revealed the dramatic loss of semi-natural habitats and declines in the quality of remaining calcareous grassland sites, however a critical question remains; what can be done about it? Chapter 5 suggested that nitrogen deposition and grazing management were key factors influencing vegetation communities in calcareous grassland. Since nitrogen deposition is a national issue, it is difficult to resolve this driver at an individual site level, however the grazing management could be addressed. Chapters 5 and 6 have revealed the importance of having sufficient grazing pressure across the different seasons, which is also echoed in other studies (Walker and Pinches 2011, Stroh et al. 2017). This has led to the establishment of a grazing experiment at Parsonage Down NNR and Martin Down NNR in 2018 and 2017, respectively. The aim of the experiment is to assess whether the introduction of spring (Parsonage Down) and summer (Martin Down) grazing can improve the quality of the sward, to reverse vegetation changes detected in Chapter 5 of this thesis. To test this I have set up three different treatments with three replicates at each site (each plot ca. 1 ha); (1) spring/summer grazing every alternate year, (2) spring/summer grazing every year and (3) business as usual, i.e. the control, with a break from the treatments every three years (Figure 7.1). Before the experiment commenced baseline vegetation surveys were conducted and these continued annually in June/July at both sites, thereby assessing the effect of summer grazing from the previous year at Martin Down and for Parsonage Down grazing occurred a couple of months beforehand in April. Five quadrats are assessed within each 1 ha plot, with the location recorded using a DGPS (Leica Zeno 20, © 2017 Leica Geosystems AG) accurate to ± 3cm. This allows accurate re-location each year, thus overcoming any of the issues outlined in section 7.4.2, as well as making repeat surveys more accessible in the future. The influence of such treatments is likely to take many years before any changes are detected, however preliminary data from each site shows increases in species richness following the implementation of the experiment, particularly where spring/summer grazing is applied every year (treatment 2) compared with the business as usual scenario (3) (Figure 7.2).



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 7.1 The location of Martin Down (A) and Parsonage Down (B), southern England. The layout of the experimental plots (ca. 1ha) at Martin Down and Parsonage Down are shown in C and D respectively, where 1 = spring/summer grazed every alternate year, 2 = spring/summer grazed every year and 3 = “business as usual”.

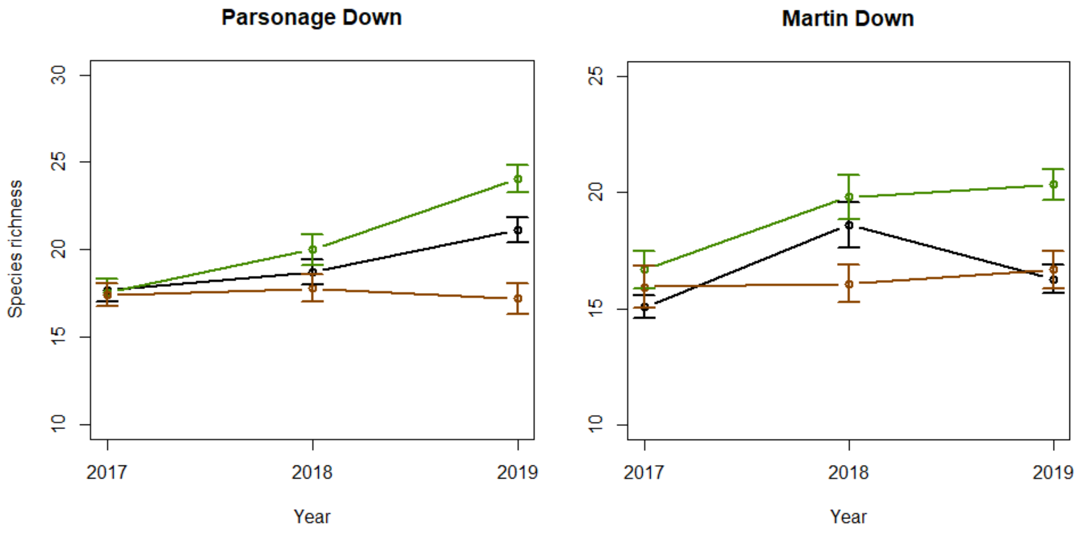


Figure 7.2 Mean species richness ± SE for 45 quadrats (1 m x 1 m) in 2017 (baseline), 2018 and 2019 at Parsonage Down and Martin Down, southern England, across the three treatments; (1) spring/summer grazed every alternate year (black), (2) spring/summer grazed every year (green) and (3) business as usual (brown).

7.6. CONCLUSIONS

Biodiversity is declining at a considerable rate and there is no evidence of this slowing. If we are to halt these declines, we need a greater understanding of the drivers of change that have occurred in the past. The research presented in this thesis demonstrates the value of using long-term data over multiple time periods to assess the major drivers of biodiversity decline. I reveal the dramatic loss of semi-natural habitats in southern England and, for the first time, identify temporal and spatial patterns behind these losses for multiple habitats within a landscape. When assessing the impact of habitat loss and degradation in relation to detecting extinction debts, I show that incorporating past species richness data is essential when analysing habitats which have undergone moderate degradation. This thesis also demonstrates the complex patterns arising from vegetation change over time, but also emphasises the advantage of having data from additional time periods, which allowed drivers to be assessed more effectively. In conclusion, the results from this thesis suggest that continued long-term monitoring and assessment over multiple time periods is essential for understanding the drivers of change in semi-natural habitats and for informing land management policies and decisions aimed at mitigating negative impacts.

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APPENDIX A

Supplementary Information for Chapter 2

A.1 Validation of time-series

Since the methodology I used for classifying habitats in the later periods (1990 and 2015 used the CEH Land Cover Maps), was quite different from the previous time points, I performed validation to assess the accuracy and consistency of the time series across all periods. I used a number of spatial datasets, including Natural England's Priority Habitats Inventory (PHI) (Natural England 2015), recent aerial photography (© ESRI World Imagery), Ordnance Survey (OS) 1:25,000 Colour Raster (Ordnance Survey 2017), as well as survey data from the 2000s. The PHI is a spatial dataset that describes the geographic extent and location of Natural Environment and Rural Communities Act (2006) Section 41 habitats of principal importance in England (Natural England 2015). Firstly, site locations were intersected with the PHI layer, to identify the priority habitat present, if any. Over 70% of sites had consistent habitat allocations across both the Land Cover Map 2015 (LCM2015) (Rowland et al. 2017) and PHI, as determined by matching the datasets using Table A.1a. For sites which didn't match, I manually checked through individual sites using a mixture of aerial photography (© ESRI World Imagery) and the OS 1:25,000 Colour Raster. The OS 1:25,000 Colour Raster was particularly useful for checking ponds and rivers which were not detected by the LCM2015, whilst the aerial photography highlighted small areas of woodland often found on the edges of fields and were thus classified incorrectly as improved grassland or arable in the LCM2015. The remaining 250 sites which were not consistent across the two datasets, were assigned improved grassland by the LCM2015, however the LCM2015 is known to have some difficulty differentiating between improved grassland, calcareous grassland and neutral grassland (Rowland et al. 2017). Where aerial photos could not be used to distinguish the habitat of these 250 sites, I used Natural England's Designated Sites database (Natural England 2017) to reveal the broad habitat for these individual sites. Only 112 sites were not consistent across the LCM2015 and PHI, nor could they be identified using the OS maps, aerial photography or the designated sites data. For these 112 sites I used the PHI habitat where the coverage was greater than 50%, whilst those with less than 50% remained as improved grassland.

I also utilised re-survey data for three habitat types; calcareous grassland, heathland and woodland, which were re-surveyed in 2009, 2010 and 2008, respectively, see Newton et al. (2012), Diaz et al., (2013), Keith et al. (2011, 2009) for further details. Over 90% of the 84 woodland re-survey sites matched the classification designated by the LCM2015. For the few sites where this was not the case, these were adjusted to reflect the woodland re-survey habitat, because these were physically visited in 2008, which is thus more reliable than the LCM2015. Over 76% of the 131 heathland sites were consistent with the classification assigned by the LCM2015. Similarly, for those which didn’t match the re-survey data, these were changed to reflect the heathland re-survey habitat. Note that not all heathland sites re-surveyed in 2010 remained as heathland (Diaz et al. 2013). Unless otherwise stated, for example “recent restoration/clearance of scrub” etc, the re-survey habitat was also presumed for 1990. For the calcareous grassland re-survey, only 30% of 83 sites were consistent with the LCM2015, however this was later explained by the fact that although sites were identified as calcareous grassland in 2009, many of the sites had reduced dramatically in size, to such a point where the main habitat was in actual fact the habitat classified by the LCM2015. This was checked using recent aerial photography (© ESRI World Imagery) and consequently these sites remained assigned to the habitat first identified using the LCM2015. Additionally, many of the calcareous grassland sites which were resurveyed in 2009, had seen an increase in more competitive species typical of mesotrophic grasslands due to eutrophication and management changes (Newton et al. 2012) and would therefore be classified as improved grassland in the LCM2015. Where sites were not consistent between the two datasets, but clearly only one main habitat existed, these sites were adjusted to reflect the calcareous grassland resurvey designation.

Table A.1a Broad habitat type matching with the Land Cover Map 2015 and Natural England's Priority Habitats Inventory.

Land Cover Map Habitat	Priority Habitats
Freshwater	Validated by OS maps
Arable and horticulture	NA
Fen, marsh and swamp	Lowland fens, Reedbeds, Coastal saltmarsh
Acid grassland	Lowland dry acid grassland
Calcareous grassland	Lowland calcareous grassland
Improved grassland	NA, Good quality semi-improved grassland
Neutral grassland	Lowland meadows
Dwarf Shrub Heath	Lowland heathland
Inland rock	NA
Saltwater	Mudflats, coastal saltmarsh, NA
Littoral sediment	Coastal vegetated shingle, Coastal sand dunes, Maritime cliff and slope
Saltmarsh	Coastal saltmarsh, Reedbeds, Mudflats
Supra-littoral rock	Maritime cliff and slope
Supra-littoral sediment	Maritime cliff and slope
Urban	NA
Suburban	NA
Broadleaved, mixed and yew woodland	Deciduous woodland
Coniferous woodland	NA, Deciduous woodland (when mixed)

A.2 Differences in the sizes of sites

The size variation for sites which remained and those that were lost in Dorset between 1930 and 2015 in each semi-natural habitat type can be seen in Figure A.2a. To determine if stand size influenced whether a site was likely to remain or not in Dorset between 1930 and 2015, I performed a Mann-Whitney U test for each of the six habitat types. I found significant differences in the area of sites which were lost versus those which remained for broadleaved woodland, calcareous grassland, fen, marsh and swamp and heathland (Table A.2a). The difference however was variable between habitat types. In broadleaved woodland and calcareous grassland sites, sites which were lost tended to be larger than those which remained, whereas for fen, marsh and swamp and heathland it was the smaller sites which were lost.

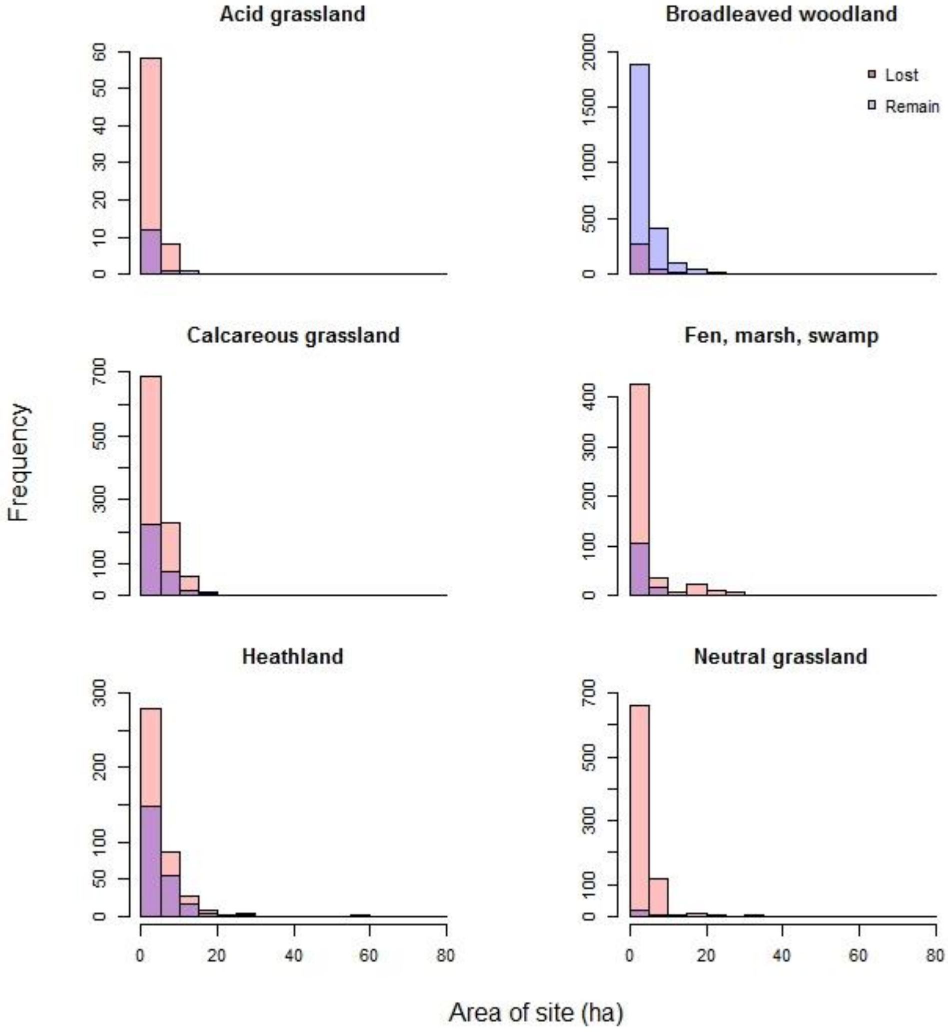

Figure A.2a Histograms of site size for remaining and lost sites for each semi-natural habitat type (acid grassland, broadleaved woodland, calcareous grassland, fen, marsh and swamp, heathland, neutral grassland) in Dorset between 1930 and 2015.

Table A.2a Mean ± SE area for sites which have remained and were lost in Dorset between 1930 and 2015, with Mann-Whitney U test results for acid grassland, broadleaved woodland, calcareous grassland, fen, marsh and swamp, heathland and neutral grassland.

	Remain	Lost	W	*p*
Acid grassland	8.64 ± 4.14	2.48 ± 0.24	108	0.434
Broadleaved woodland	3.65 ± 0.10	4.83 ± 0.40	120149	0.027
Calcareous grassland	4.53 ± 0.31	5.53 ± 0.25	45696	0.017
Fen, marsh, swamp	2.99 ± 0.41	2.02 ± 0.16	6013	0.020
Heathland	7.26 ± 0.74	5.41 ± 0.39	10222	0.010
Neutral grassland	2.45 ± 0.72	2.96 ± 0.11	2363	0.260

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APPENDIX B

Supplementary Information for Chapter 3

B.1 Justification of methodology for 1980 land use/land cover (LULC) map

To generate the 1980 LULC map for Dorset, I also modelled landscape change using the generated 1950 map as the baseline, rather than the Land Cover Map 2015 (LCM2015) (Rowland et al. 2017). The same methodology of using the habitat time-series from Chapter 2 was employed to quantify the LULC change and generate the transition matrix, except this time I evaluated the change between 1950 and 1980, rather than 2015 to 1980. The LULCs which increased between 1950 and 1980 were consistent with the changes between 1930 and 1950, which included arable, improved grassland, coniferous woodland and urban. The same environmental factors (Table 3.1) were analysed using a logistic regression for the increasing LULCs, as described in the main text.

The resulting map output can be seen in Figure B.1a, alongside the 1980 map output produced using the LCM2015. The key difference between the 1980 output maps is the large difference in arable land that has been predicted from the two different baseline maps. To determine which map is likely to be the most accurate I used an alternative data source to validate the area of arable across Dorset in the 1980s. For this I used the Agriculture Census data which revealed the area of "total crops" in 1981 in 2 km x 2 km grid squares (data obtained from http://edina.ac.uk/agcensus/, accessed 24/10/18). I calculated the area of arable in both of the 1980 maps using the same 2 km x 2 km grid squares. To determine which of the 1980 maps matched the Agricultural Census best, I compared histograms and examined the association between each map with the Agricultural Census data using Spearman's Rank Correlation. The histogram of the area of arable from the 1980 map created from LCM2015 (1980 from 2015) matches more closely with the Agricultural Census data compared with the 1980 map created from the 1950 (1980 from 1950) (Figure B.1b). The 1980 from 1950 histogram shows a more even frequency spread across the different areas, whilst the 1980 from 2015 shows a large proportion of 2 km x 2 km grid squares have smaller areas of arable, as in the

Agriculture Census dataset. This is further confirmed by the stronger association detected between the 1980 from 2015 data and the Agricultural Census data (R_s = 0.66), compared with the 1980 from 1950 (R_s = 0.58) (Figure B.1c).

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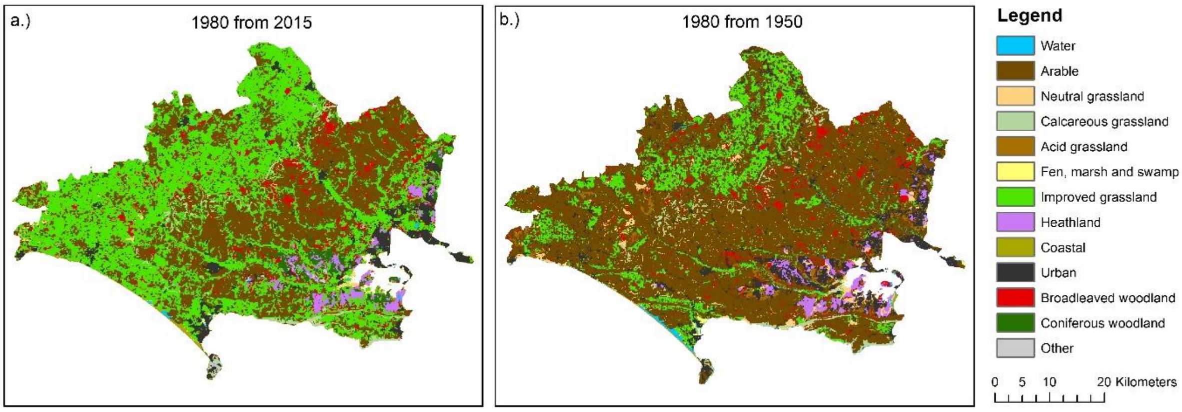

Figure B.1a Dorset LULC maps for 1980 created from a.) the Land Cover Map 2015 (Rowland et al. 2017) and b.) the modelled 1950 map.

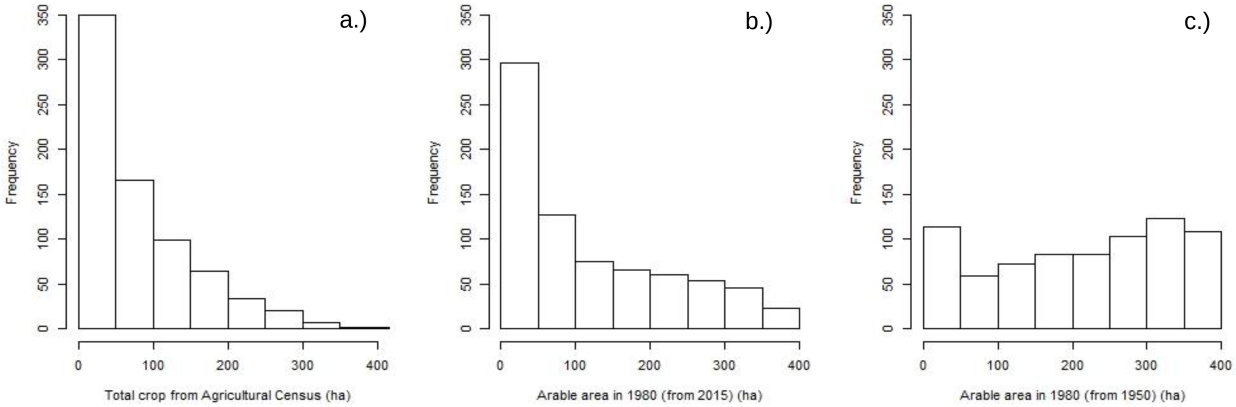

Figure B.1b Histograms showing the area of arable in Dorset in a.) 1981 from the Agricultural Census, b.) 1980 created from the Land Cover Map 2015 (Rowland et al. 2017) and c.) 1980 created from the modelled 1950 map.

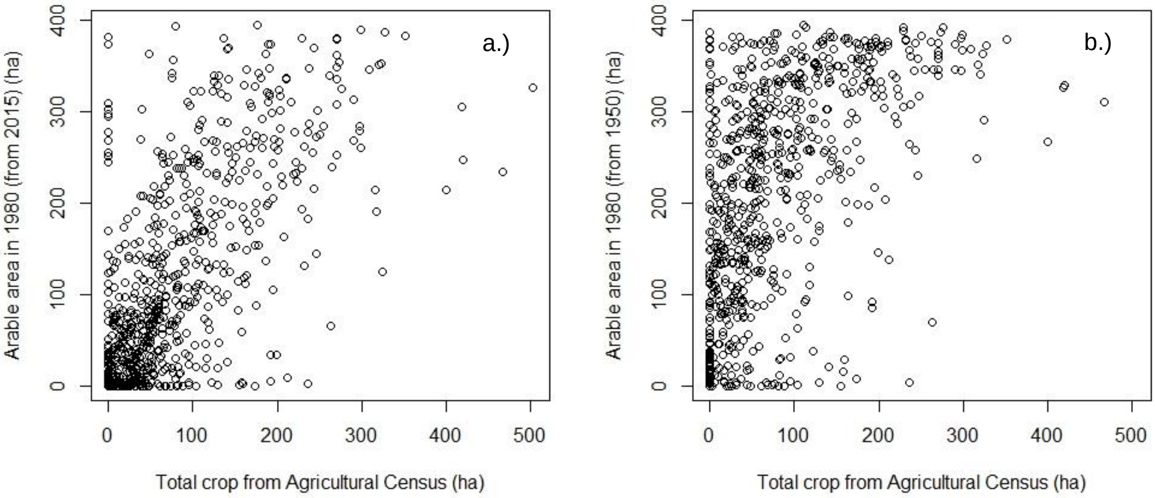

Figure B.1c Scatterplots showing the relationships between total crop in the Agricultural Census and arable in 1980 created from a.) the Land Cover Map 2015 (Rowland et al. 2017) and b.) the modelled 1950 map.

Table B.2 Transition matrix required for the InVEST Scenario Generator Tool (Sharp et al. 2016). This example is for the first cross-validation dataset for the creation of the 1950 map.

Id	Name	Water	Arable	Neutral	Calcareous	Acid	Fen, marsh, swamp	Improved	Heathland	Coastal	Urban	Broadleaved	Coniferous	Percent Change	Area Change	Priority	Proximity
1	Water	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Arable	0	0	0	0	0	0	0	0	0	0	0	0	122	0	8	1000
3	Neutral grassland	0	9	0	0	0	0	9	0	0	4	4	0	0	0	0	0
4	Calcareous grassland	0	9	0	0	0	0	9	0	0	4	4	6	0	0	0	0
5	Acid grassland	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0
6	Fen, marsh, swamp	0	9	0	0	0	0	8	0	0	4	8	4	0	0	0	0
7	Improved grassland	0	0	0	0	0	0	0	0	0	0	0	0	0	15100	7	0
8	Heathland	0	5	0	0	0	0	8	0	0	4	4	8	0	0	0	0
9	Coastal	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0
10	Urban	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
11	Broadleaved woodland	0	6	0	0	0	0	7	0	0	0	0	6	0	0	0	0
12	Coniferous woodland	0	0	0	0	0	0	0	0	0	0	0	0	1275	0	5	1000

Table B.3 Transition matrix required for the InVEST Scenario Generator Tool (Sharp et al. 2016). This example is for the first cross-validation dataset for the creation of the 1980 map.

Id	Name	Water	Arable	Neutral	Calcareous	Acid	Fen, marsh, swamp	Improved	Heathland	Coastal	Urban	Broadleaved	Coniferous	Other	Percent Change	Area Change	Priority	Proximity
1	Water	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Arable	0	0	7	8	0	0	7	0	0	0	0	0	0	5	0	7	1000
3	Neutral grassland	0	0	0	0	0	0	0	0	0	0	0	0	0	375	0	9	1000
4	Calcareous grassland	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	9	1000
5	Acid grassland	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Fen, marsh, swamp	0	0	0	0	0	0	0	6	6	0	0	0	0	62	0	9	1000
7	Improved grassland	0	9	8	9	0	8	0	0	5	0	0	0	0	0	0	0	0
8	Heathland	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	9	1000
9	Coastal	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	7	1000
10	Urban	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0
11	Broadleaved woodland	0	0	7	7	0	9	0	7	0	0	0	0	0	0	0	0	0
12	Coniferous woodland	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	1000
13	Other	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX C

Supplementary Information for Chapter 4

C.1 Extinction debt analyses using additional time periods

I tested for extinction debt using additional time periods (1950 and 1980) for the Past Habitat method. To determine the habitat patch area for heathland in 1950 rather than using the 1950 landscape map produced by Ridding et al. (2020a) (Chapter 3), which remained largely unchanged since the 1930s, despite the fact that a considerable area of heathland was lost during this period (Ridding et al. 2020b, Chapter 2), I manually digitised heathland areas from a historical maps series, Ordnance Survey (OS) Great Britain 1:25,000, 1937-1961 (Ordnance Survey 1961). No extinction debt was evident for woodland in any of the time periods using the Past Habitat method, since the ΔAICc < 2 for each of the species groups (Table C.1a). The same pattern was identified for the two specialist groups for heathland, however for all species the 1930 habitat area for heathland explained the contemporary species richness better than the habitat area in 1950, 1980 or 2015, with AICc increasing with time, which therefore suggests an extinction debt. For calcareous grassland, the 1930 habitat area remained the time period which explained contemporary species richness the best, thus an extinction debt is evident for this habitat. The support for the model did not necessarily increase with time for strict habitat specialists, whereas for habitat specialists and all species there was no difference between the models in 1950, 1980 and 2015.

It was also possible to analyse 1950 as another time point for the Stable Habitats method. I did this only for calcareous grassland, since dividing heathland and woodland into stable and unstable patches for 1950 produced greatly unbalanced sample sizes, which were unsuitable for analysis. Calcareous grassland was divided into 30 stable and 36 unstable sites, with an average of 46% and 11% retained respectively, between 1950 and 2015. Strict habitat specialists did not reveal an extinction debt, whilst the results for habitat specialists and all species was less clear (Table C.1b). The past model (where the past habitat area is used as a predictor) indicated there was no evidence of an extinction debt, whilst the current model (based on contemporary area as a predictor) suggested there was. Helm et al. (2006) stated that the two models bracket the magnitude of the extinction debt, where the model based on past landscape structure probably gives an overestimate of extinction debt, whilst the model based on the contemporary landscape probably gives an underestimate.

Table C.1a Extinction debt evaluated using the "Past Habitat" method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. The exponentiated coefficient and standard error along with the p-value for the patch variable, AICc and R^2 values are presented for each regression model.

	Species groups	Year	Coefficient	SE	P	AICc	R^2
Calcareous grassland	Strict habitat specialist	1930	1.29	1.07	<0.001	544.22	0.044
	Strict habitat specialist	1950	1.01	1.05	0.895	558.67	0.018
	Strict habitat specialist	1980	1.06	1.03	0.031	553.91	0.027
	Strict habitat specialist	2015	1.05	1.04	0.183	556.90	0.022
	Habitat specialist	1930	1.25	1.05	<0.001	661.87	0.047
	Habitat specialist	1950	1.02	1.03	0.548	682.45	0.017
	Habitat specialist	1980	1.03	1.02	0.185	681.04	0.019
	Habitat specialist	2015	1.01	1.03	0.662	682.62	0.017
	All species	1930	1.08	1.03	0.029	709.16	0.025
	All species	1950	0.98	1.02	0.335	713.10	0.019
	All species	1980	0.98	1.01	0.081	711.01	0.022
	All species	2015	0.98	1.02	0.312	713.00	0.019
Heathland	Strict habitat specialist	1930	1.34	1.26	0.204	183.31	0.120
	Strict habitat specialist	1950	1.35	1.22	0.135	182.64	0.123
	Strict habitat specialist	1980	1.29	1.16	0.081	181.78	0.127
	Strict habitat specialist	2015	1.28	1.15	0.080	181.77	0.127
	Habitat specialist	1930	1.29	1.16	0.081	259.29	0.153
	Habitat specialist	1950	1.30	1.14	0.043	258.08	0.157
	Habitat specialist	1980	1.23	1.10	0.025	257.12	0.160
	Habitat specialist	2015	1.23	1.09	0.025	257.13	0.160
	All species	1930	1.30	1.07	<0.001	561.23	0.036
	All species	1950	1.21	1.05	<0.001	565.75	0.029
	All species	1980	0.99	1.04	0.884	579.22	0.005
	All species	2015	1.00	1.03	0.927	579.24	0.005
Broadleaved woodland	Strict habitat specialist	1930	0.98	1.04	0.628	485.95	0.017
	Strict habitat specialist	1950	0.98	1.04	0.558	485.55	0.018
	Strict habitat specialist	1980	0.97	1.04	0.406	485.85	0.018
	Strict habitat specialist	2015	0.96	1.04	0.361	485.36	0.019
	Habitat specialist	1930	0.96	1.02	0.054	626.85	0.021
	Habitat specialist	1950	0.95	1.02	0.031	625.90	0.023
	Habitat specialist	1980	0.94	1.03	0.025	625.56	0.023
	Habitat specialist	2015	0.94	1.03	0.018	625.90	0.024
	All species	1930	0.94	1.01	0.001	780.09	0.102
	All species	1950	0.93	1.02	<0.001	777.49	0.105
	All species	1980	0.93	1.02	<0.001	777.28	0.106
	All species	2015	0.92	1.02	<0.001	777.28	0.107

Table C.1b Extinction debt evaluated using the “Stable Habitats” method for calcareous grassland between 1950 and 2015, for the three species groups (strict habitat specialist, habitat specialist and all species) in Dorset. The exponentiated coefficient and standard error, and R^2 values are presented for each regression model. Extinction debt is calculated as the difference between the numbers of predicted and observed plant species, alongside the range and the p-value resulting from a Wilcoxon test comparing the two. Those in bold reveal where an extinction debt is suggested.

Species groups	Model	Coefficient	SE	R^2	Extinction debt		
Strict habitat specialist	Current	1.25	1.11	0.034	2.09	(-10.22 ~ 18.79)	0.074
Strict habitat specialist	Past	1.02	1.06	0.016	-1.48	(-13.72 ~ 13.78)	0.181
Habitat specialist	Current	**1.22**	**1.08**	**0.042**	**5.23**	**(-15.66 ~ 30.82)**	**0.006**
Habitat specialist	Past	1.03	1.04	0.020	0.66	(-19.21 ~ 24.38)	0.625
All species	Current	**1.06**	**1.05**	**0.044**	**5.81**	**(-32.21 ~ 40.94)**	**0.018**
All species	Past	0.98	1.03	0.040	0.90	(-35.83 ~ 32.31)	0.499

C.2 Stable habitat method with 20% threshold

The division of stable and unstable habitats using the “Stable Habitats” method produced very unbalanced sample sizes when employing a threshold of 20% for heathland and broadleaved woodland. For calcareous grassland this resulted in 30 stable habitats and 36 unstable habitats. Extinction debts were identified for all three species groups within calcareous grassland, whereby the observed plant species richness values were significantly higher than predicted (Table C.2a).

Table C.2a Extinction debt evaluated using the “Stable Habitats” method with a 0.2 threshold for calcareous grassland for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. Model indicates whether past or current patch area was used to predict contemporary species richness. The exponentiated coefficient and standard error, and R^2 values are presented for each regression model. Extinction debt is calculated as the difference between the numbers of predicted and observed plant species, alongside the range and the p-value resulting from a Wilcoxon test comparing the two. Those in bold reveal where an extinction debt is suggested.

Species groups	Model	Coefficient	SE	R^2	Extinction debt		
Strict habitat specialist	Current	**1.63**	**1.14**	**0.073**	**5.33**	**(-7.04 ~ 22.20)**	**<0.001**
Strict habitat specialist	Past	**1.69**	**1.12**	**0.114**	**7.87**	**(-4.23 ~ 23.90)**	**<0.001**
Habitat specialist	Current	**1.54**	**1.10**	**0.086**	**10.32**	**(-11.64 ~ 36.37)**	**<0.001**
Habitat specialist	Past	**1.61**	**1.09**	**0.144**	**14.96**	**(-6.47 ~ 39.74)**	**<0.001**
All species	Current	**1.21**	**1.06**	**0.062**	**13.37**	**(-26.94 ~ 52.30)**	**<0.001**
All species	Past	**1.24**	**1.05**	**0.094**	**20.20**	**(-19.92 ~ 58.24)**	**<0.001**

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APPENDIX D

Supplementary Information for Chapter 5

Table D.1 Qualitative grazing management data collected for Parsonage Down between 1930 and 2011.

Type	Management	Source
Cattle		
1930 -1972	The down was grazed by a mixture of Aberdeen Angus, Belted Galloways and Blue Greys being ranched over more than 400 ha. Stocking levels were carefully controlled.	Pywell et al. (1995); Wild (1988)
1973 -1990	Site is grazed by 330 to 350 beef cattle, including 90 breeding cows. Only the 90 cows would have grazed the down 365 days a year. Hardy breeds were used since they remain out in winter and calve on the open down (Hereford crosses pre-dominate, while characteristics are also derived from Longhorn, Angus and British White). There is also a small herd of Longhorn cattle. Hay and straw are used to feed in winter in less-species rich areas. The cows are served by a Charolais bull which produces a quick growing calf suitable for market at all times of the year. Calves are typically produced in spring, weaned and taken to the stocking yards in January.	Pywell et al. (1995)
2003	90 cows supplementary feeding stopped on feed bank SSSI (Castle) & haylage fed on backup ground – cattle out-wintered on SSSI – approx. 50 tonnes of forage fed	Roger Marris (Senior Reserve Manager until September 2016) and Simon Hope (current Reserve Manager)
2008	Cattle numbers reduced to 75 cows & brought off SSSI into straw corral at Cherry Lodge Farm in December & returned to SSSI (Castle) in March for calving	Roger Marris (Senior Reserve Manager until September 2016) and Simon Hope (current Reserve Manager)
2011	75 cows housed for winter from December & then turned out onto backup ground (Lodge) in March for calving & then trickled back onto SSSI (Castle) as they calve in April & May	Roger Marris (Senior Reserve Manager until September 2016) and Simon Hope (current Reserve Manager)
Sheep		
Pre 1979	Grazing with both cattle and sheep, with stocking levels carefully controlled	Wild (1988)
1970-1990	430 Scotch half-bred ewes are crossed with Suffolk rams for fat and ewe lamb production. Ewes with twin lambs were put on the down in April, then lambs were sold from May to October. The rams are put with the ewes from December until March when all the sheep come off the down. Hay and straw are used to feed from December until April in less-species rich areas; these areas are then harrowed in May.	Pywell et al. (1995)
1999	380 Scotch half-bred lambing ewes – singles placed on SSSI from March onwards	Roger Marris (Senior Reserve Manager until September 2016) and

		Simon Hope (current Reserve Manager)
2003	250 Scotch half-bred lambing ewes – singles placed on SSSI from March onwards	Roger Marris (Senior Reserve Manager until September 2016) and Simon Hope (current Reserve Manager)
2008	80 lambing ewes on backup ground, 100 Suffolk x Mule ewe lambs bought in, in September to graze SSSI (Castle) all year round, sold a year later as yearlings to be replaced by a new group of 100 ewe lambs	Roger Marris (Senior Reserve Manager until September 2016) and Simon Hope (current Reserve Manager)

Table D.2 Soil properties measured from 11 positions at two depths across four transects at Parsonage Down NNR in 1970, 1990 and 2016.

			L.O.I (%)			pH			K (mg/kg)			Ca (mg/kg)			Mg (mg/kg)			PO4-P (mg/kg)			N%		
Transect	Position	Sample Depth	1970	1990	2016	1970	1990	2016	1970	1990	2016	1970	1990	2016	1970	1990	2016	1970	1990	2016	1970	1990	2016
1	21S	0_5	26	27	28.9	7.5	7.6	7.6	160	180	140	11710	6600	10800	200	190	207	24	17	15.9	1.05	1.2	1.41
1	21S	5_10	23	20	21.8	7.5	7.8	7.6	110	110	93.7	10840	5900	9050	160	110	125	19	12	10.8	0.97	0.99	1.1
1	60S	0_5	27	26	25.7	7.6	7.9	7.6	160	190	219	12040	6400	10300	200	150	196	28	22	14	1.11	1.2	1.32
1	60S	5_10	23	20	17	7.5	7.6	7.6	140	120	113	10620	5700	7400	120	83	106	17	18	9.73	0.95	1	0.87
1	10N	0_5	24	28	25.6	7.5	7.8	7.6	190	440	127	11490	7400	9680	250	180	190	NA	23	11.9	1.03	1.3	1.22
1	10N	5_10	23	23	18.9	7.6	7.8	7.7	140	180	72.4	11240	6500	8130	160	120	85.2	19	14	8.78	0.97	1.1	0.92
1	50N	0_5	25	27	24.6	7.5	7.7	7.6	300	170	124	11370	7600	9690	200	220	157	35	23	12.3	1.1	1.3	1.18
1	50N	5_10	22	23	18.4	7.6	7.8	7.6	120	110	70.7	10540	6500	8060	120	110	87.7	17	17	9.36	0.96	1.1	0.92
2	8S	0_5	29	30	26.9	7.4	7.7	7.6	240	250	151	12890	7900	10500	250	260	185	26	39	11.1	1.3	1.3	1.27
2	8S	5_10	24	25	24.4	7.4	7.8	7.6	160	150	126	12660	7600	9680	160	250	125	19	23	9.89	1.1	1.1	1.17
2	50S	0_5	27	27	26.9	7.3	7.9	7.5	220	170	114	12850	7300	10300	320	200	155	29	21	10	1.2	1.2	1.26
2	50S	5_10	25	22	22.9	7.4	7.9	7.6	120	130	81.8	11330	6700	9370	200	120	97.2	19	16	8.6	1	1	2.21
2	51N	0_5	28	32	25.7	7.5	7.6	7.5	210	210	136	12730	8000	9930	280	220	217	28	31	12.8	1.3	1.5	1.26
2	51N	5_10	24	31	21.2	7.5	7.9	7.6	140	100	83.1	10730	6300	8470	180	100	141	23	14	10.1	0.99	1.1	1.06
3	60S	0_5	24	23	25.8	7.4	8	7.6	130	150	105	10750	6400	9850	160	160	154	20	17	11.7	1.1	1.1	1.24
3	60S	5_10	NA	NA	21.7	NA	NA	7.6	NA	NA	64.9	NA	NA	8760	NA	NA	89.4	NA	NA	10.6	NA	NA	1.06
3	7S	0_5	25	24	25.8	7.5	8	7.6	170	180	134	12100	7400	10100	200	180	162	17	19	11.2	0.98	1.2	1.15
3	7S	5_10	NA	NA	23.5	NA	NA	7.6	NA	NA	81.8	NA	NA	9420	NA	NA	106	NA	NA	10.1	NA	NA	1.02
4	60S	0_5	30	27	25.5	7.5	7.8	7.6	250	170	116	12820	7500	9620	230	270	143	28	31	12	1.3	1.3	1.27
4	60S	5_10	23	22	18.9	7.6	7.9	7.7	130	92	68.5	10570	7000	8220	120	150	76.9	15	21	9.15	1.02	1.1	0.95
4	8S	0_5	26	28	25.8	7.5	7.8	7.6	180	200	135	12490	8300	10250	250	200	228	28	25	11.9	1.1	1.2	1.18
4	8S	5_10	21	24	24.4	7.7	7.7	7.6	120	160	106	11350	7300	9060	150	140	156	6	20	9.73	0.86	1.1	1.07

Table D.3 Detailed soil methodology for each soil property; pH, loss on ignition (LOI), exchangeable Potassium (K), Magnesium (Mg) and Calcium (Ca), Phosphate (PO_4-P) and total Nitrogen (N). All soil samples were passed through a 2 mm sieve and air dried prior to chemical analysis.

Soil property	Description
pH	Soil samples were added to ultra-pure water and then were mixed vigorously. After leaving the solution to settle for 20 minutes, the pH was measured using an automated Skalar electrode calibrated at pH 4, pH 7 and pH 10. The pH electrode was inserted into the liquid solution at the top of the settled sample and agitated gently to remove air bubbles. After being left for 5 minutes, a reading is taken.
LOI	Soil samples were air-dried at 40°C and ball milled, then dried for a further 3 hrs at 105°C. A sample was accurately weighed and placed in the muffle furnace at 550°C for 3 hrs, cooled and weighed again. In house reference material was used with each batch of samples.
Total N	Air dried (at 40°C) samples were ball milled and then oven dried at 105°C (± 5°C) for a minimum of 3 hours and then cooled. Each sample (20 mg) was enclosed in a tin sheet and analysed for total N using a Vario EL (Elementar Analsensysteme GmbH, Hanau, Germany). The instrument was calibrated using a working standard (Acetanilide) with approximate concentrations of 10.4% total N.
K, Mg, Ca	Air dried (40°C) and sieved soils were digested with 1 M ammonium acetate at pH 9. The samples were extracted for one hour using an end-over-end shaker, and then were filtered using a pre-rinsed Whatman number No. 44. The extracts were analysed for Calcium, Magnesium, Potassium, using a Perkin Elmer model 7300DV Inductively Coupled Plasma-Optical Emission Spectrometer (ICP-OES). With each batch of samples, a blank and two in-house reference materials were run. The elements were quantified using matrix matched external standards. The limits of quantification were 0.171, 0.318 and 0.009 and limits of detection were 0.059, 0.108 and 0.006 for Ca, K and Mg, respectively.
PO_4-P	Two grams of air dried soil samples were extracted in 40 ml Olsen's reagent (0.5 M NaHCO3 at pH 8.5) for 30 minutes in a mechanical end over shaker. Samples were then filtered through a Whatman 44 filter paper and the solution was analysed for PO4-P using a Seal Analytical AA3 segmented flow analyser connected to a chart recorder. In the

instruments the samples were mixed in the flow channel with an acidic ammonium molybdate and potassium antimony tartrate to form a complex with phosphate. This complex was reduced with ascorbic acid to develop a molybdenum blue colour. The reaction was temperature controlled to 40°C using a water bath and the colour was measured at 880nm. For quality control two different reference material are run every 10 samples and the samples were quantified using external calibration standards.

Table D.4 Grid references (EPSG:27700) for the start and end of the four transects recorded at Parsonage Down in 1970, 1990 and 2016.

Transect	Start	End
1	SU0419441445	SU0421141424
2	SU0418941394	SU0420241365
3	SU0418041303	SU0419341297
4	SU0417441293	SU0418841280

Table D.5 Frequency (%) of vascular plant species surveyed from 115 quadrats in 1970, 1990 and 2016 at Parsonage Down. Significance of change between 1970-1990 and 1990-2016 assessed by Chi-square tests (adjusted for multiple comparisons using Benjamini and Hochberg (1995)). CG2 positive indicator species from Common Standards Monitoring (JNCC 2004).

Species	Indicator	1970	1990	2016	1970 - 1990 change	1990 - 2016 change
Increasing						
Agrostis stolonifera		37.39	33.91	50.43	Decrease	Increase**
Anthoxanthum odoratum		0.87	0.00	0.87	Decrease	Increase
Bromopsis erecta		0.00	0.00	17.39	No change	Increase
Lolium perenne		0.00	4.35	34.78	Increase	Increase***
Phleum bertolonii		6.09	6.09	9.57	No change	Increase
Schedonorus pratensis		0.00	0.00	8.70	No change	Increase
Trisetum flavescens		0.00	0.87	0.87	Increase	No change
Carex flacca		92.17	85.22	95.65	Decrease	Increase
Cerastium fontanum		0.00	0.00	0.87	No change	Increase
Clinopodium vulgare		0.00	0.00	0.87	No change	Increase
Coeloglossum viride		0.00	0.00	0.87	No change	Increase
Crataegus monogyna		0.87	0.00	0.87	Decrease	Increase
Crepis capillaris		3.48	0.00	5.22	Decrease	Increase
Galium album		0.00	0.00	0.87	No change	Increase
Galium verum		53.91	61.74	55.65	Increase	Decrease
Helianthemum nummularium	X	37.39	30.43	44.35	Decrease	Increase*
Medicago lupulina		8.70	27.83	20.00	Increase***	Decrease
Ononis repens		0.87	0.00	6.96	Decrease	Increase
Ononis spinosa		0.00	15.65	2.61	Increase	Decrease**
Serratula tinctoria	X	0.87	0.87	4.35	No change	Increase***
Succisa pratensis	X	57.39	86.09	87.83	Increase***	Increase
Viola hirta		0.00	0.00	4.35	No change	Increase
Decreasing						
Avenula pratensis		78.26	80.87	51.30	Increase	Decrease**
Avenula pubescens		73.04	32.17	22.61	Decrease***	Decrease
Briza media		80.00	84.35	70.43	Increase	Decrease
Cynosurus cristatus		61.74	29.57	25.22	Decrease***	Decrease
Dactylis glomerata		75.65	70.43	65.22	Decrease	Decrease
Deschampsia cespitosa		1.74	0.00	0.00	Decrease	No change
Festuca ovina		95.65	100.00	82.61	Increase	Decrease
Festuca rubra		2.61	0.87	0.00	Decrease	Decrease
Holcus lanatus		1.74	0.87	0.00	Decrease	Decrease
Koeleria macrantha		83.48	84.35	48.70	Increase	Decrease***
Poa pratensis		0.87	0.00	0.00	Decrease	No change
Carex caryophyllea		70.43	72.17	12.17	Increase	Decrease***
Carex humilis		61.74	39.13	39.13	Decrease**	No change
Achillea millefolium		0.00	0.87	0.00	Increase	Decrease
Anacamptis morio		2.61	0.00	0.00	Decrease	NA
Anthyllis vulneraria	X	0.00	2.61	0.00	Increase	Decrease
Asperula cynanchica	X	11.30	6.09	0.00	Decrease	Decrease*
Bellis perennis		0.87	0.00	0.00	Decrease	No change
Campanula glomerata	X	20.00	12.17	0.00	Decrease	Decrease**
Campanula rotundifolia		43.48	26.96	0.87	Decrease*	Decrease***
Centaurea nigra		75.65	66.09	8.70	Decrease	Decrease***
Centaurea scabiosa		6.96	4.35	0.00	Decrease	Decrease
Cirsium acaule	X	65.22	60.00	47.83	Decrease	Decrease
Cirsium arvense		0.00	6.09	0.00	Increase	Decrease*

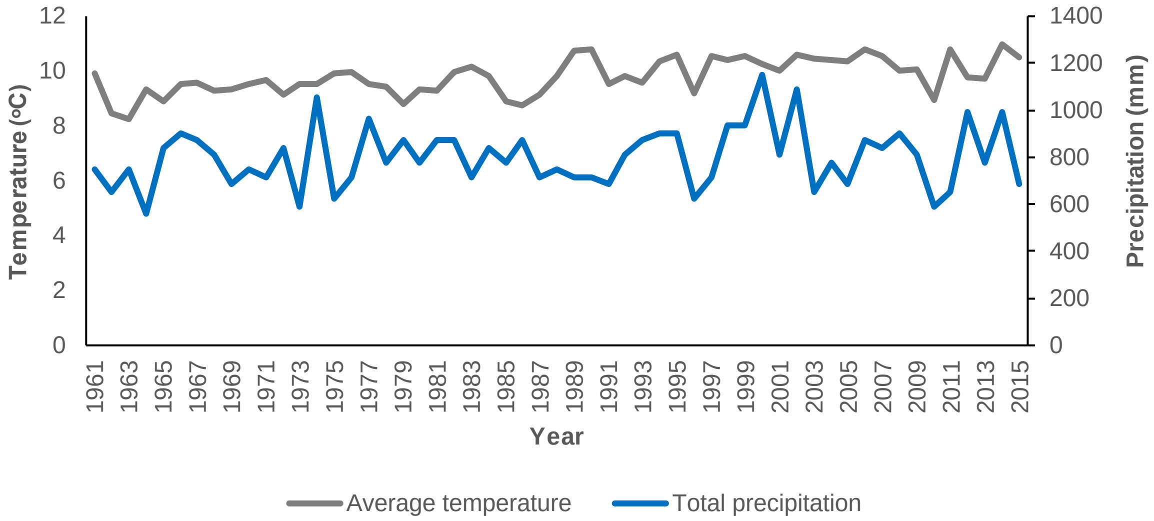
Euphrasia nemorosa		32.17	13.04	0.00	Decrease**	Decrease***
Filipendula vulgaris	X	68.70	53.04	55.65	Decrease	Increase
Gentianella amarella	X	0.00	1.74	0.00	Increase	Decrease
Hippocrepis comosa	X	3.48	0.00	0.00	Decrease	No change
Leontodon hispidus	X	88.70	70.43	43.48	Decrease	Decrease**
Leucanthemum vulgare	X	12.17	11.30	1.74	Decrease	Decrease**
Linum catharticum	X	18.26	23.48	6.96	Increase	Decrease**
Lotus corniculatus	X	69.57	77.39	53.04	Increase	Decrease*
Luzula campestris		5.22	5.22	0.00	No change	Decrease*
Neotinea ustulata		1.74	0.00	0.00	Decrease	No change
Onobrychis viciifolia		37.39	28.70	31.30	Decrease	Increase
Picris hieracioides		11.30	15.65	0.00	Increase	Decrease***
Pilosella officinarum	X	4.35	0.00	0.87	Decrease	Increase
Pimpinella saxifraga		59.13	58.26	4.35	Decrease	Decrease***
Plantago lanceolata		89.57	85.22	66.09	Decrease	Decrease
Plantago media	X	70.43	61.74	19.13	Decrease	Decrease***
Polygala calcarea	X	5.22	0.87	0.00	Decrease	Decrease
Polygala vulgaris	X	0.87	0.87	0.00	No change	Decrease
Poterium sanguisorba	X	88.70	96.52	87.83	Increase	Decrease
Primula veris	X	20.87	16.52	15.65	Decrease	Decrease
Prunella vulgaris		29.57	27.83	6.96	Decrease	Decrease***
Ranunculus bulbosus		85.22	19.13	40.00	Decrease***	Increase***
Scabiosa columbaria	X	36.52	85.22	18.26	Increase***	Decrease***
Scorzoneroides autumnalis		13.04	33.91	0.00	Increase***	Decrease***
Senecio jacobaea		2.61	6.96	0.00	Increase*	Decrease*
Spiranthes spiralis		1.74	0.00	0.00	Decrease	No change
Taraxacum agg		6.96	6.09	2.61	Decrease	Decrease
Thesium humifusum		0.87	3.48	0.00	Increase**	Decrease
Thymus polytrichus	X	6.09	3.48	4.35	Decrease	Increase
Trifolium campestre		2.61	0.00	0.00	Decrease	No change
Trifolium pratense		75.65	60.87	35.65	Decrease	Decrease**
Trifolium repens		77.39	30.43	4.35	Decrease***	Decrease***
Veronica chamaedrys		0.87	0.00	0.00	Decrease	No change

(*P < 0.05, **P < 0.01, ***P <0.001)

Table D.6 Redundancy analysis (RDA) results for soil variables recorded at 33 quadrats at Parsonage Down in 1970, 1990 and 2015.

Soil Variable	Df	Variance	F	P
pH	1	3.22	1.37	0.119
PO_4-P	1	7.33	3.12	0.001***
N	1	3.51	1.49	0.088
K	1	1.27	0.54	0.959
Ca	1	2.39	1.02	0.429
Mg	1	2.75	1.17	0.231
LOI	1	2.80	1.19	0.266

Figure D.7 Average temperature and total precipitation at Parsonage Down between 1961 and 2015 (Robinson et al. 2017).



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APPENDIX E

Supplementary Information for Chapter 6

Table E.1 Availability of vegetation and grazing data between 1979-1994 (excluding 1992) and 2002-2010 at Martin Down, where V and G indicate vegetation and grazing data respectively.

Plot	Com	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	2002	2003	2004	2005	2006	2007	2008	2009	2010
1	5b	VG	VG	VG	VG	G	G	G	VG	G	G	G	G	G		G	VG	G	G	G	G	G	G	G	G	G	VG
2	6b	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	VG
3	6b	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	G		G	VG	G	G	G	G	G	G	G	G	G	VG
5	6a	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	VG		G	VG	G	G	G	G	G	G	G	G	G	VG
6	6a	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	VG		G	VG	G	G	G	G	G	G	G	G	G	VG
13	11a	VG	VG	VG	VG	G	G	G	G	VG	G	G	G	G		G	VG	G	G	G	G	G	G	G	G	G	VG
15	20a	V	V	V		V		G	G	VG	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	VG
16	20a	V	V	V				G	G	VG	G	G	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
19	4a	VG	VG	VG	VG	G	G	G	VG	G	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	VG
20	4a	VG	VG	VG	VG	G	G	G	VG	G	G	VG	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
24	21			V	V		G	G	VG	G	G	VG	G			G	G	G	G	G	G	G	G	G	G	G	VG
25	21			V	V		G	G	VG	G	G	VG	G		V	G	G	G	G	G	G	G	G	G	G	G	VG
26	4b	G	G	G	VG	G	G	G	VG	G	G	G	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
27	4b	G	G	G	VG	G	G	G	VG	G	G	G	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
30	7b	G	G	G	G	G	VG	G	VG	VG	G	G	G	G			G		G	G	G	G	G	G	G	G	VG
31	7b	G	G	G	G	G	VG	G	VG	VG	G	G	G	G			G		G	G	G	G	G	G	G	G	VG
42	11a	G	G	G	G	G	G	VG	G	VG	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	G
53	6b	G	G	G	G	G	G	G	G	VG	G	G	V	G		G	G	G	G	G	G	G	G	G	G	G	G
54	21						G	G	G	VG	VG	G	V	G		G	G	G	G	G	G	G	G	G	G	G	G

Table E.2. Positive indicators for CG3 and CG2 grasslands extracted from the Common Standards Monitoring for lowland grasslands (JNCC 2004), which have been recorded at Martin Down between 1979-2010.

Species	CG3	CG2
Anthyllis vulneraria	Y	Y
Asperula cynanchica	Y	Y
Brachypodium pinnatum	Y	
Bromopsis erecta	Y	
Cirsium acaule	Y	Y
Filipendula vulgaris	Y	Y
Galium verum	Y	Y
Gentianella amarella	Y	Y
Gentianella anglica	Y	Y
Helianthemum nummularium	Y	Y
Pilosella officinarum	Y	Y
Hippocrepis comosa	Y	Y
Leontodon hispidus	Y	Y
Leontodon saxatilis	Y	Y
Leucanthemum vulgare	Y	Y
Linum catharticum	Y	Y
Lotus corniculatus	Y	Y
Plantago media	Y	Y
Polygala calcarea	Y	Y
Polygala vulgaris	Y	Y
Primula veris	Y	Y
Sanguisorba minor	Y	Y
Scabiosa columbaria	Y	Y
Succisa pratensis	Y	Y
Thymus polytrichus	Y	Y

Table E.3 Model coefficients, 2.5 and 97.5% quantiles for species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance with year and total average sheep days within spring, summer, autumn and winter in the previous three years as explanatory variables. Coefficients for species richness and indicator richness have been exponentitated.

Model	Explanatory variable	Median	2.5% quantile	97.5% quantile	*P*-value	AIC
Species richness	Year	1.058	1.000	1.120	0.049	428.616
	Spring grazing	0.977	0.919	1.040	0.463	
	Summer grazing	1.016	0.958	1.073	0.576	
	Autumn grazing	0.996	0.942	1.053	0.875	
	Winter grazing	0.971	0.920	1.027	0.300	
Species diversity	Year	0.884	0.050	1.719	0.034	375.441
	Spring grazing	-0.242	-1.084	0.601	0.536	
	Summer grazing	0.244	-0.669	1.156	0.579	
	Autumn grazing	0.103	-0.741	0.948	0.814	
	Winter grazing	-0.684	-1.502	0.134	0.092	
Indicator richness	Year	1.035	0.929	1.152	0.528	355.996
	Spring grazing	1.026	0.922	1.133	0.623	
	Summer grazing	1.027	0.919	1.141	0.626	
	Autumn grazing	1.048	0.942	1.160	0.379	
	Winter grazing	0.945	0.850	1.048	0.294	
Indicator abundance	Year	-0.005	-0.036	0.025	0.701	-52.503
	Spring grazing	0.008	-0.023	0.039	0.588	
	Summer grazing	-0.012	-0.046	0.023	0.496	
	Autumn grazing	0.001	-0.031	0.032	0.940	
	Winter grazing	-0.018	-0.049	0.012	0.224	
Grass abundance	Year	0.012	-0.020	0.044	0.431	-54.548
	Spring grazing	0.015	-0.016	0.046	0.341	
	Summer grazing	0.000	-0.033	0.034	0.916	
	Autumn grazing	0.010	-0.022	0.041	0.528	
	Winter grazing	0.026	-0.004	0.056	0.082	
Forb abundance	Year	-0.006	-0.035	0.024	0.690	-72.026
	Spring grazing	-0.011	-0.038	0.017	0.410	
	Summer grazing	0.008	-0.019	0.035	0.539	
	Autumn grazing	-0.001	-0.029	0.027	0.943	
	Winter grazing	-0.021	-0.047	0.006	0.146	

Table E.4 Model coefficients, 2.5 and 97.5% quantiles for species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance with total average sheep days within spring, summer, autumn and winter in the previous year as explanatory variables. Coefficients for species richness and indicator richness have been exponentiated.

Model	Explanatory variable	Median	2.5% quantile	97.5% quantile	*P*-value	AIC
Species richness	Spring grazing	0.979	0.934	1.027	0.372	559.450
	Summer grazing	0.997	0.951	1.045	0.903	
	Autumn grazing	1.019	0.974	1.064	0.411	
	Winter grazing	0.988	0.944	1.034	0.603	
Species diversity	Spring grazing	-0.300	-1.088	0.489	0.430	505.503
	Summer grazing	0.245	-0.565	1.054	0.556	
	Autumn grazing	0.647	-0.087	1.381	0.092	
	Winter grazing	-0.110	-0.822	0.602	0.736	
Indicator richness	Spring grazing	0.995	0.904	1.091	0.909	452.629
	Summer grazing	1.040	0.945	1.140	0.408	
	Autumn grazing	1.060	0.978	1.145	0.149	
	Winter grazing	1.017	0.940	1.099	0.663	
Indicator abundance	Spring grazing	-0.003	-0.030	0.024	0.844	-88.055
	Summer grazing	0.003	-0.026	0.032	0.827	
	Autumn grazing	0.010	-0.014	0.034	0.402	
	Winter grazing	0.002	-0.021	0.025	0.846	
Grass abundance	Spring grazing	0.007	-0.023	0.038	0.632	-71.637
	Summer grazing	-0.012	-0.043	0.019	0.477	
	Autumn grazing	-0.004	-0.032	0.025	0.810	
	Winter grazing	0.013	-0.015	0.040	0.374	
Forb abundance	Spring grazing	-0.002	-0.028	0.024	0.888	-94.065
	Summer grazing	0.014	-0.012	0.040	0.287	
	Autumn grazing	0.007	-0.018	0.032	0.581	
	Winter grazing	-0.013	-0.038	0.011	0.332	

REFERENCES FOR APPENDIX E:

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